Durham E-Theses

The evolution of body size and sexual size dimorphism in primates

PEPLOE, JOSEPH,RICHARD

The evolution of body size and sexual size dimorphism in primates

Joe Peploe

Abstract

Primates vary widely in respect to body mass, as well as sexual size dimorphism. Despite largely being considered the result of sexual selection, the processes that give rise to sexual size dimorphism are still widely debated, with a number of alternative theories having been and still being proposed. Relatively recent studies have found that allometric relationships among primates follow two prominent and widely cited "rules" of evolutionary biology, Rensch's rule and Cope's rule. Using phylogenetic comparative methods that enable the detection of long-term trends from extant data, and by looking at male and female evolutionary history independently, I test the idea that sexual selection for increased male size is not only the primary mechanism behind sexual size dimorphism in primates, but also the observed trends of Cope's and Rensch's rule. I find that although multiple processes may lead to sexual size dimorphism in primates, the most extreme cases, those observed in the catarrhines, are most likely the result of selection for larger males. The most notable example of this occurred early on in catarrhine evolution, with several lineages subsequently undergoing further selection on male size. I also find that selection for increased male size in catarrhines as the most likely cause behind the pattern of Rensch's rule and Cope's rule observed in primates, suggesting that these "rules" should not in fact be considered allometric rules, but are instead trends that result directly from sexual selection for larger male size. I also find that species adopting polygynous and polygynandrous mating systems are significantly more sexually dimorphic in size than monogamous and polyandrous species. These results open up intriguing new avenues of future study in which the relative roles of natural selection and sexual selection in the evolution of morphological traits can be teased apart, and further light shed on questions that have pervaded evolutionary biology for centuries.

THE EVOLUTION OF BODY SIZE AND SEXUAL SIZE DIMORPHISM IN PRIMATES

Joe Peploe

MRes

Department of Anthropology

Durham University

2023

Table of contents

1. Introduction

1.1.　　　Purpose and aims of study

Varying widely across the animal kingdom, body size is a central aspect of adaptation, influencing just about every aspect of biology, ecology and evolution. With correlations between body size and multiple other life history traits having been observed throughout the history of evolutionary biology, it is no wonder that understanding the evolution of body size plays a key role in macroecology and macroevolutionary studies (e.g. Peters, 1983; Cooper and Purvis, 2010). How and why changes in body size occur and the processes that underpin its evolution have been the subject of much interest for as long as the field has been practiced, and the methods used to study it have undergone continuous adaptation.

Crucial to adaptation, body mass evolution in many cases may represent responses to changing natural selection pressures (Maurer et al., 1992), and such adaptations can often be studied through comparative methods between species to attempt to understand the driving forces behind its evolution. However, body mass does not only differ between species, but also within species, most notably between males and females (Fairbairn, 1997). The difference in size between the sexes observed in many animal lineages is referred to as sexual size dimorphism and is just one type of sexual dimorphism commonly observed throughout the animal kingdom. Despite widespread attention dating as far back as before Charles Darwin, who considered that most sexual dimorphism is owing to sexual selection (Darwin, 1871), the exact mechanisms and processes that give rise to sexual size dimorphism are still debated today, with a number of competing theories.

Amongst primates, a diverse order of mammals, body mass varies widely, ranging from as small as 30g, to as large as 170kg (Smith and Jungers, 1997; Rowe and Myers, 2017). The evolution of which is thought to be influenced by a number of factors, including the latitudinal distribution, habitat type, locomotion type and the social structure of a given species (Dunham et al., 2013; Gallen-Acedo et al., 2019). Primates are also among the most sexually dimorphic of mammalian orders,

with multiple morphological traits differing in several species (Kappeler, 1990; Lindenfors and Tullberg, 1998; Plavcan, 2012). Males in the most dimorphic species reach sizes that are twice as large as females. However, there is also much variation in the degree of sexual size dimorphism, both between species and across clades, with many species lacking size dimorphism altogether (Smith and Jungers, 1997). Thus, in order to understand body size evolution, we must separate males and females and consider how both natural selection and sexual selection have influenced the evolution of each and draw upon the differences between them to better understand historical patterns.

The variation and the degree of sexual size dimorphism observed in primates makes them an excellent group in which to study the patterns of body mass evolution between males and females. Relatively recent studies have found evidence of heterogenous evolutionary rates of body mass in primates (Venditti et al, 2011; Elton and Dunn, 2020), as well as differing rates between the sexes in at least some clades (Elton and Dunn, 2020). Such findings are suggestive of multiple routes towards primate body size diversity, and potentially differential selection acting upon the sexes. No study, however, has so far examined the contribution of varying rates of male and female body size evolution to sexual dimorphism across the whole primate order, or indeed any mammalian order.

Similarly recent studies have also found that the evolution of body size among primates follows two prominent and widely cited "rules" of evolutionary biology; Rensch's rule, which postulates that sexual size dimorphism increases with body mass in species in which males are the larger sex, as in primates (Rensch, 1959; Abouheif and Fairbairn, 1997; Gordon, 2006; Cardini and Elton, 2008), and Cope's rule, describing a tendency for organisms to evolve towards larger sizes over evolutionary time (Smith and Cheverud, 2002; Gordon, 2006; Baker at al., 2015). All of these recent findings taken together indicate that delving deeper into the patterns of body mass evolution between the sexes as well as between the various clades of primates may help to shed light on the mechanisms that drive such observed trends, and in answering the questions that have been debated for centuries about the drivers of body size evolution and sexual size dimorphism.

Here I build on recently developed comparative methods to examine patterns of body mass evolution in primates, with a focus on understanding the ways in which males and females contribute to both overall size and sexual size dimorphism. I analyse body mass data within a phylogenetic framework, estimating rates of evolution for both males and females across the entire order, identifying branches of the phylogenetic tree in which rates of evolution differ between the sexes. Drawing upon Cope's rule and Rensch's rule, I will be addressing the question of what drives the evolution of sexual size dimorphism, and what role sexual selection plays in this. I will also be examining the validity of both "rules" in respect to primates, and attempting to answer the question of whether sexual selection is a driving mechanism behind the observation of these trends within primates.

1.2. Background context

1.2.1. The comparative approach and Cope's rule

It is unavoidable in evolutionary biology to make comparisons, be it between species, or between individuals of the same species. Such comparisons allow evolutionary biologists to identify patterns and trends suggestive of underlying mechanisms and causes, from which hypotheses can be proposed (Nelson, 1970). From comparisons it is also possible to observe similarities and differences between species. These similarities and differences can represent adaptations that have been shaped by selection, and it is these adaptations that form the framework of the comparative approach (Russell, 1916; Martinez, 2018).

From the time of Charles Darwin, who made comparisons between similar species on the Galapagos Islands to mold his theory of evolution (Darwin, 1859), the comparative method has been the most common approach used to attempt to answer questions about patterns of evolutionary change through time. Much of what we know today has come from these early observational studies. Over time, the development of methods that couple these intrinsic observations about evolution with statistical processes to formally test hypotheses have cemented the position of comparative studies at the forefront of evolutionary biology research (Harvey and Pagel, 1991; Nunn, 2011).

The traditional approach was to analyse trends treating extant species as independent data points, inferring evolutionary processes from the patterns observed. Such studies are considered non-directional, as they do not take into consideration the relationships between lineages, known as phylogenies. As methods for reconstructing phylogenies and ancestral states have developed and improved, directional studies that make use of the phylogenetic history of species to determine direction and rates of evolutionary change between ancestors and descendants have been made possible (Falsenstein, 1985; O'Meara, 2012).

Directional studies taking into account phylogenetic histories are crucial, as they enable the alleviation of a major problem that has pervaded the traditional approach to comparative biology; that of similarities between closely related species owing to the inheritance of traits from common ancestors (Pagel et al., 2003). This shared inheritance means that species within a lineage are not independent, and so when treated as independent data points in a statistical analysis may lead to the overestimation of the true number of degrees of freedom and inaccurate interpretations of evolutionary processes (Harvey and Pagel, 1991; Meade and Pagel, 2017).

More recently, non-directional and directional methods have begun to merge, with developments that allow for the consideration of phylogenies in comparisons between contemporary species, it has become possible to discern long term evolutionary trends from extant data only (Harvey and Pagel, 1991; Venditti et al., 2011; Baker et al., 2015). Given the sparsity of the fossil record, such a possibility opens exciting new opportunities to explore patterns of evolutionary change in a wide variety of traits.

Regarding body size, one of the most common evolutionary patterns observed is a general trend towards increased size over time. This trend has been termed Cope's rule, named after the American paleontologist Edward Drinker Cope (Stanley, 1973), and coined by German evolutionary biologist Bernhard Rensch (Rensch, 1948). Cope's rule is over a century old, but there is still debate as to its validity. Studies across a wide range of taxa have yielded mixed results, with support being found in several instances, including among dinosaurs (Benson et al., 2017; Hone et al., 2005) and mammals (Alroy, 1998; Baker at al., 2015; Clauset

and Erwin, 2008), and the opposite observed in others (Jablonski, 1997; Butler and Goswami, 2008). Sceptics of Cope's rule have explained the observed trend as a statistical artefact of increasing variance in body size within clades arising from small ancestors (Gould, 1997).

For Cope's rule to reflect active selection for larger size, it is necessary for large size to provide a general increase in fitness across lineages, and for these increases in fitness to outweigh any fitness costs of large size (Hone and Benton, 2005). General fitness advantages thought to result from larger size include increased defense against predation, a greater range of acceptable food sources, increased success in mating and intraspecific competition and increased tolerance to environmental extremes. Proposed costs of large size include an increased total requirement of food and water, longer developmental time and increased susceptibility to extinction (Hone and Benton, 2005; Baker et al., 2015; McKinney, 1997, Charnov and Berrigan, 1993).

In oviparous groups, such as insects, females are often the larger sex. Larger females benefit from being able to produce more eggs (Kingsolver and Pfennig, 2004). In mammals on the other hand, female reproductive costs often increase with body size, with females in the largest species being less fecund. This suggests that fecundity selection may act in the opposite direction in mammals as it does in oviparous groups (Cassini, 2017).

Given the intrinsic advantages large size may provide, Cope's rule might be the result of repeated responses to new natural selection pressures, with generations benefitting from the fitness advantages of increased size over previous generations. However, large size is also widely considered to be a consequence of sexual selection, as larger males out compete their smaller counterparts in intra-specific competition for mating success (Fairbairn, 1997; Gordon, 2006; Lindenfors et al., 2007). Accordingly, despite a long history of attention, the mechanisms explaining the operation of Cope's rule are not fully understood, thus closer looks at the patterns of body mass evolution throughout the animal kingdom may well be needed to further understand the trend.

Mammalian orders represent valuable groups in which to study body mass evolution, owing to the wide range of sizes observed amongst extant species

(Jones et al., 2009). Over the course of their 165-million-year history, mammals have evolved to span almost eight orders of magnitude in size (Venditti et al., 2011), consequently providing a plentiful past through which to explore evolutionary theories of how species evolve to fill new ecological niches and come to exist in such a myriad of sizes and shapes.

For the majority of their history, mammals were mostly small, shrew-like creatures, remaining so up until the end of the Cretaceous period (Kemp, 2005). The subsequent radiation of the mammals occurred after the mass extinction of the non-avian dinosaurs approximately 65 million years ago, in what is known as the Cretaceous-Paleogene extinction event (Kemp, 2005). It is believed that this emptied the ecological spaces that had before been occupied primarily by the dinosaurs, allowing the surviving mammals to thrive and diversify over the following Paleocene and Eocene epochs through a process known as adaptive radiation, in which organisms undergo rapid diversification from an ancestral species (Simpson, 1953). This process necessitates that species experience accelerated rates of evolution early in the history of a lineage ("early burst"), before subsequent periods of relative stability in which rates of evolution and speciation slow (Simpson, 1953; Venditti et al., 2011). However, more recently, adaptive radiation has been challenged as the predominant process by which speciation and morphological diversity arise, with studies finding that such early bursts of evolution are far rarer than thought, and competing processes such as selective peak, in which species evolve via a series of small genetic steps towards a fitness optimum, may play a more prominent role (Venditti et al., 2011; Harmon et al., 2010). Whatever the processes, in the intervening years since the extinction of the non-avian dinosaurs, mammals have diversified widely in regard to body size, as lineages as large as the Elephentidae on land, and the Cetaceans of the oceans have emerged (Sahney et al., 2010).

That the Cetaceans have evolved to such large sizes illustrates the importance of ecological factors in the evolution of body size: life in water places less of a constraint on body size than does land (Goldbogen, 2018). Such constraints vary among environments on land as well however, with wide open landscapes giving rise to some of the largest terrestrial mammals on earth (Fisher et al., 2011). As an order that primarily evolved in arboreal environments, primate body size has also

been influenced by ecology. A number of species have descended from the trees to assume terrestrial lives, and in doing so many have evolved to larger sizes than their arboreal counterparts (Milton and May, 1976; Leutenegger and Cheverud, 1982), although there are exceptions, with several large primates maintaining mainly arboreal lifestyles. These ecological influences again demonstrate the complexity of body size evolution.

The pattern of increased size through time (Cope's rule) originated from observations in the mammalian fossil record (Alroy, 1998), but has historically proven difficult to demonstrate through phylogenetic comparative methods using data from extant species (Monroe and Bokma, 2010). However, using a recently developed approach, Baker et al., (2015) found trends in mammalian body mass evolution compatible with Cope's rule for the first time from extant species alone (Baker et al., 2015). The approach used detected regions of the tree that have undergone exceptionally fast or slow rates of change, stretching or compressing individual branches according to the rate of evolution (variable rates model) (Venditti et al., 2011). The study found that increased rates of evolution in body size above that expected under a Brownian motion model of evolution (a model in which trait value changes direction randomly over time) across the mammalian phylogeny were disproportionately associated with increases in size – but not decreases, therefore suggesting active selection for increased size, in ten of eleven orders for which sufficient data was available, including the primates (Baker et al., 2015), the Diprotodontia being the only order in which a trend towards increasing size was not found. In reconstructing ancestral states, the authors found that estimates from the variable rates model more accurately predicted the sizes of ancestral states than the Brownian motion model, thus variable rates models may be more accurate than single rate models and therefore preferable in the absence of fossil data (Baker et al., 2015).

Within the order primates, contrarily to Baker et al, previous studies have found opposing patterns using data from the fossil record (Soligo, 2001; Soligo, 2006). Soligo (2006) investigated whether there is a directional trend in body size evolution in primates and plesiadapiforms, an extinct group thought to be a sister taxon to primates (Silcox et al., 2017), by analysing the global fossil record. The findings of the study suggested that whilst plesiadapiforms did show a trend

11

compatible with Cope's rule, primates showed no such trend. Significant shifts in body size between major adaptive radiations were observed, but not an intrinsic trend for increasing size within lineages (Soligo, 2006).

These conflicting studies show the juxtaposition between comparative methods using extant data and those using fossil data. The primate fossil record is relatively sparse, with no more than 7% of all primate species that have ever existed being recovered from the fossil record (Soligo, 2006; Tavare et al., 2002). Given this current sparsity, the finding of Baker et al., (2015) in demonstrating the ability to discern long term evolutionary trends from extant data is one that opens considerable new avenues in the study of evolutionary processes, particularly in studies in which the inclusion of data from the fossil record is not possible, such as this one, whereby reliable estimates of body size for both males and females does not exist for the vast majority of known fossil species.

What these studies do share, however, is that they both demonstrate the differences that can be found between lineages, with differing trends being observed across even closely related clades. In wide scale studies it is possible that certain lineages in which significant trends are detected may have the effect of dragging entire orders along with them, falsely implying that the given trend is more widespread than it may actually be (Lindenfors et al., 1998). It is therefore critical to recognise the importance of focusing on individual clades when conducting expansive studies in order to more accurately understand the observation of evolutionary patterns.

The above studies highlight how phenotypic evolution does not follow a homogenous pattern, with some clades undergoing significantly faster rates of evolution than others (Venditti et al., 2011; Revell et al., 2008; Barton and Venditti., 2014; Baker et al., 2016), as quantified by Haldane in the first half of the 20th century (Haldane, 1937). Given that there is also much intra-specific variation in body size between males and females throughout the animal kingdom, as well as amongst primates, along with the varying life histories and selection pressures males and females are subject to, it is likely that patterns of evolution also vary between the sexes.

1.2.2. Sexual size dimorphism and Rensch's rule

Sexual dimorphism has been studied and written on since the time of Aristotle, who postulated that divergences in morphology are associated with differences in behaviour. Two thousand or so years later Charles Darwin remarked extensively on the subject in his book *The Descent of Man*, originating the concept of sexual selection, which he theorised was the leading evolutionary cause of dimorphism (Darwin, 1871).

Commonly observed sexually dimorphic characteristics include size, coloration, ornamentation and weaponry. In many cases these dimorphic traits appear not to benefit survival, or, in the cases of coloration and ornamentation, may often be detrimental to survival (Fisher, 1930). The observation of traits seemingly counterproductive to survival is what led Charles Darwin to propose sexual selection, in which individuals of one sex compete for access to members of the other sex, as the driving mechanism behind the evolution of such conspicuous traits (Darwin, 1871). In many of the species in which sexual dimorphism is observed, it is males that tend to exhibit the more elaborate of morphological characteristics, as individuals compete with one another. This is true in most part for mammals as well as birds, but not necessarily other clades. The competition that takes place between males in these species may be intrasexual, whereby physical combat determines mating success, or intersexual, in which one sex, most commonly females, choose members of the other sex. Intrasexual competition results in sexually selected weaponry as well as increased size in the competing sex, and intersexual competition in coloration and ornamentation as a means by which to increase attractiveness to the selecting sex (Darwin, 1871; Proctor et al., 2012).

Since Darwin, the idea of sexual selection as the cause of sexual dimorphism has garnered a lot of support, with several studies evidencing its role in the evolution of sexual dichromatism (sexual dimorphism in the form of coloration), ornamentation and weaponry (Gadgil, 1972; Kodric-Brown, 1985; Plavcan, 2001; Tobias et al., 2012; Cooney et al., 2020). However, the role of sexual selection in sexual size dimorphism has received more mixed support, with a number of alternative factors considered to influence size differences (Plavcan, 2001).

13

Sexual dimorphism may also arise from natural selection. Mechanisms such as sexual niche separation, contrasting response to resource pressures and fecundity selection may all play a role in influencing sexual size dimorphism (Cassini, 2017; Cassini, 2020). Mammals are relatively unusual in that males tend to be larger than females, in many other animal groups, like insects, fish and most reptiles for example, it is females that are most often the larger sex (McLean et al., 2018; Lindenfors et al., 2007). In such animals, fecundity, as defined by the maximum potential reproductive output of a female throughout her lifetime, is highly correlated with female fitness, and thus a positive correlation between body size and fecundity often exists (Cassini, 2017). In these instances, the larger the female, the more fecund she tends to be. Larger females generally carry larger eggs, which are associated with a higher number and better quality of offspring (Borghezan, 2019), and the female-biased sexual size dimorphism observed is the result, as males are not subject to the same selection pressure (Cassini, 2017). However, in mammals it has been demonstrated that female reproductive costs increase with body size, and that almost all female life history parameters related to fecundity are slower or energetically more costly in larger species (Lindenfors et al., 2007). Because of these costs, it is thought that in mammals fecundity selection may act in the opposite direction, favouring smaller body size in females (Martin, 1984). It has therefore been proposed that the male-biased sexual size dimorphism observed in mammals may be the result of fecundity selection limiting female body size in a trade-off between survival and reproduction, with males able to evolve to larger sizes without the same constraints (Martin et al., 1994; Cassini, 2017; Elton and Dunn, 2020).

Across the primate order there is a wide degree of sexual size dimorphism, The most dimorphic of species are found among the catarrhine primates, which are also the largest overall of all primates. Males of such species as the gorillas and mandrills are as much as twice the size of females (Smith and Jungers, 1997; Rowe and Myers, 2017). Despite alternative theories, sexual selection is still widely regarded to be a leading cause of the increased sexual size dimorphism seen in many primate species, particularly that seen in haplorrhines, a group containing both the catarrhines of Africa and Asia, and platyrrhines of South America, whilst excluding strepsirrhines (Lindenfors, 1998; Gordon, 2006).

The intensity of sexual selection acting on male primates is thought to depend upon the mating system a species has adopted, being of the highest intensity in polygynous species, and the least in monogamous. Polygynous species usually involve a dominant male, who has access to all the females within a group and must compete with other males to maintain dominance. It is therefore expected that in such species there is a higher degree of intrasexual competition between males. Where males compete via combat for access to females, it is usually the larger males that are the victors and consequently mate with the most females and have the most offspring (Clutton-Brock et al., 2006). In monogamous species, males and females remain pair bonded, and as a result these species tend to exhibit less intrasexual competition and a lower degree of sexual selection (Kappeler, 1990; Plavcan, 2012; Cassini, 2020). A number of species exhibit polygynandrous systems, in which both males and females mate with multiple mates. Finally, some species are polyandrous, where females mate with multiple males (Rowe and Myers, 2017). Many species of primate may often change mating system also, depending on certain factors, such as group size and operational sex-ratio (Kappeler and Van Schaik, 2002; Opie et al., 2012; Kappeler and Pozzi, 2019). Nonetheless, the idea that sexual size dimorphism in primates is the consequence of sexual selection acting to increase male size has received much support from studies demonstrating a greater degree of sexual size dimorphism in species with polygynous mating systems (Cassini, 2020; Weckerly, 1998; Plavcan, 2012). Expected increases in sexual selection are associated with increases in sexual size dimorphism through the increase of male body size more so than female (Lindenfors, 1998).

Lending further support to the role of sexual selection in the evolution of sexual size dimorphism, male and female primates often differ in traits other than size also, including in canine length (Harvey et al., 1978; Leutenegger and Cheverud, 1985; Plavcan, 2001). Canine length, an example of weaponry, is highly associated with male-male competition, with dimorphism significantly correlated with the intensity of competition (Plavcan and Van Schaik, 1997). Unsurprisingly, canine dimorphism has also been found to correlate considerably with body size dimorphism (Plavcan and Van Schaik, 1997). Given the role of sexual selection in the evolution of canine dimorphism, sexual size dimorphism is also likely, in large

part, to be caused by sexual selection. In addition, many primate species also display sexual dichromatism (Bradley and Mundy, 2008; Caro, 2021). A number of lemur species are particularly dichromatic, whilst lacking any sexual size dimorphism despite polygynous mating systems (Cooper and Hosey, 2003; Rakotonirina et al., 2017). It has been posited that the lack of size dimorphism is due to reduced physical combat in lemurs, and a more significant role of female mate preference, whereby females prefer more colourful males (Cooper and Hosey, 2003). The presence of male ornamentation in primates is evidence of sexual selection being at work, however, the role it plays in the evolution of sexual size dimorphism remains a question requiring further research.

A prominent pattern relating to sexual size dimorphism is that of Rensch's rule. Proposed by Bernhard Rensch in 1950, Rensch's rule postulates that sexual size dimorphism tends to increase with average body mass in species in which males are the larger sex, but that the opposite is the case – sexual size dimorphism decreases as body mass increases – in species in which females are the larger sex (Rensch, 1950). There is much conflicting evidence as to whether Rensch's rule holds true for the majority of lineages, with support being found in many (Abouheif and Fairbairn, 1997; Smith and Cheverud, 2002; Szekely, 2004), but also several studies showing the converse, particularly in orders in which size dimorphism is female biased (Webb and Freckleton, 2007; Cooper, 2018). Within mammals, a group more commonly exhibiting male biased size dimorphism, results are similarly inconsistent, with firm evidence only being found in primates and diprotodonts (Lindenfors et al., 2007). Other studies looking at primates specifically have also shown consistency with the "rule" (Clutton-Brock et al., 1977; Smith and Cheverud, 2002; Gordon, 2006), with both body size dimorphism and canine dimorphism shown to be higher in the largest species. Studies of individual primate lineages have also found consistency with Rensch's rule among certain lineages of catarrhines, such as the guenons (Cardini and Elton, 2008), however, a weaker trend has been observed in platyrrhines (Smith and Cheverud, 2002; Gordon, 2006), and no such trend at all in strepsirrhines (Kappeler, 1990; Plavcan, 2012). Such findings again demonstrate the importance of investigating evolutionary patterns across clades, as well as the importance of controlling for phylogeny (Lindenfors and Tullberg, 2006).

Why a positive scaling relationship between body size and sexual size dimorphism should exist at all is not clear (Gordon, 2006). Several different explanations have been suggested, which Fairbairn (1997) grouped into eight categories, and Gordon (2006) subsequently condensed into three; 1) increases in body size cause or facilitate increases in sexual size dimorphism, 2) correlations of genetics or selection pressures between sexes cause changes in dimorphism and body size of both sexes when selection is applied to the size of one sex, and 3) natural selection applies differential sex-specific selection pressures resulting in changes in size and dimorphism (Gordon, 2006; Fairbairn, 1997). There is little support for a general or intrinsic relationship between sexual size dimorphism and body size, and indeed the lack of dimorphism in many lineages despite variation in mean body sizes contradicts the presence of such a relationship (Gordon, 2006).

A lack of consistency with Rensch's rule has been found in other mammalian orders, including canids, in which the prevalence of monogamy within the order has been posited as the reason (Bidau and Martinez, 2016). Such a suggestion necessarily draws sexual selection into the subject of Rensch's rule, as if sexual selection is the driving force behind sexual size dimorphism in lineages in which it is displayed, it may also be expected that dimorphism will increase in larger-bodied species. As the intensity of sexual selection increases, males will evolve at greater rates relative to females, resulting in increased sexual size dimorphism (Lindenfors, 1998).

The suggestion of sexual selection as a leading mechanism behind the observation of Rensch's rule, as well as a general pattern of increased size, poses an interesting question, one that may necessitate an intrinsic link between the two "rules".

1.2.3. Rensch's rule and Cope's rule: two sides of the same coin?

Being both allometric rules, it is not surprising that Rensch's rule and Cope's rule have been previously linked. McLain, (1993) suggested that Cope's rule may be explained by sexual selection, i.e., selection for larger males may cause an overall trend of increasing size over time (McLain, 1993). Such an explanation would necessarily link Cope's rule with Rensch's rule, as if it is males driving the

17

observation of Cope's rule, then Rensch's rule would also result, as males continue to increase in size at greater rates than females. This would lead to the largest species also being the most dimorphic.

It has previously been demonstrated by Lindenfors et al., (1998) that sexual selection is a large driving force for size evolution in both male and female haplorrhine primates. Considering the proposition that Rensch's rule is largely the result of sexual selection also (Lande, 1987; Lindenfors, 1998), Lindenfors, like McClain previously, made the observation that it is not an unreasonable hypothesis that sexual selection could be the main driver behind a general pattern of size increase (Lindenfors, 1998). As males increase in size due to sexual selection, females will also be expected to be relatively larger owing to genetic correlations. However, females will not increase in size at the same rate as males as they will not be subject to active selection and thus dimorphism will increase. If this is the case, an evolutionary pattern towards increasing size would also be one towards increasing dimorphism, consequently resulting in the same mechanisms leading to the observations of both "rules".

Using recently developed phylogenetic comparative methods that enable the detection of long-term trends, such as Cope's rule, from extant data (Baker et al., 2015), it is theoretically possible to estimate sexual size dimorphism of ancestral species. By detecting contrasting evolutionary patterns and rates of evolution between the sexes, the relative role of sexual selection in the evolution of body size and sexual size dimorphism may be determined.

1.3.   Primate phylogeny and history

Primates represent a major mammalian radiation, rich in ecological diversity. The fossil record shows primates as having been far more widely distributed than the tropical and sub-tropical regions of Asia, Central and South America and Africa that non-human primates of today are limited to, with evidence that primates were once widespread throughout Eurasia, and reached as far as North America and China (Rose, 1994). The first primates are thought to have originated and diversified soon after the Cretaceous-Paleogene extinction event around 65 million

years ago, along with many other mammalian radiations (Kemp, 2005), with the earliest unambiguous euprimate fossils (fossil forms exhibiting all of the features of modern primates) no older than 56 million years (Soligo and Smaers, 2016; Silcox, 2014). These early fossils already demonstrate the split between strepsirrhines and haplorrhines, the groups that living primates fall into, and vary in size from as small as mice to as large as domestic house cats (Silcox et al., 2007; Sussman et al., 2013).

1.3.1. Strepsirrhines

Strepsirrhines comprise the lemurs of Madagascar, along with the galagos and lorisids of Africa and Asia. Lemurs are endemic to Madagascar, thought to have evolved from loris-like ancestors sometime around 59-65 million years ago. Originating in Africa, lemurs must have at some point crossed the Mozambique Channel to arrive on the island of Madagascar (Yoder and Zang, 2004; Tattersall, 2006). Rafting, by which species cross water by drifting on tangled "rafts" of vegetation, is the most accepted explanation for how lemurs made their way across the sea. Isolated on the island, they met no competition from other arboreal mammalian species, and so over the following millions of years diversified to fill various niches, and today are divided into eight families consisting of fifteen genera (Krause, 2003).

Most lemurs are relatively small in size, but the different genera range from as small as ~30g up to ~9kg (Smith and Jungers, 1997; Rowe and Myers, 2017). However, the fossil record shows sub-fossil lemurs, such as *Archaeoindris*, reaching as large as 160kg (Godfrey et al, 2010), as large as male gorillas and many times larger than any extant species, up until as recently as two thousand years ago, shortly after humans arrived on Madagascar. It is widely believed that humans played a large role in driving these large species to extinction (Godfrey et al., 2006; Godfrey et al., 2010; Godfrey, 2016). These extremely large sub-fossil species indicate that extant species are a biased sample of the body size distribution that primates evolved to in Madagascar, and consequently, this should be borne in mind when investigating body size evolution of lemurs.

19

Modern lemurs show a lack of sexual size dimorphism, with males and females in all lineages approximating the same size, despite many species practicing a polygynous mating system (Smith and Jungers, 1997; Rowe and Myers, 2017). This lack of sexual size dimorphism has also been found to be the case in the large-bodied sub-fossil lemurs (Godfrey et al., 1993).

The lorisids are found in tropical, central Africa as well as south and southeast Asia. Today, lorisids are divided into five genera, and are typically small primates, ranging from ~100g to ~2kg (Smith and Jungers, 1997). All lorisids are nocturnal and arboreal, and like other strepsirrhines, lack any sexual size dimorphism. Although there is some evidence in the literature that suggests galagids exhibit notable dimorphism relative to other strepsirrhine species (O'Mara et al., 2012). Closely related to the lorisids, the galagos, also known as bush babies, are native to continental Africa, having split from the lorisids approximately 34-41 million years ago (Kumar et al., 2017). Six genera of galagos exist today, and like lorisids are small in size, ranging from ~50g to a little over 1kg, and are also nocturnal and arboreal (Pozzi et al., 2014).

1.3.2. Tarsiers

The other major suborder of primates are the haplorrhines, made up of the tarsiers and the simians. Tarsiers split from the simians approximately 60-70 million years ago (Kumar et al., 2017), and although once widely distributed, can now only be found in southeast Asia. In appearance, tarsiers are more similar to the lorisids and galagos than they are the simians, small in size and lacking sexual size dimorphism (Niemitz, 1984).

1.3.3. Platyrrhines

Simians consist of the platyrrhines and the catarrhines. Platyrrhines are made up of five families of primate that are found in Central and South America, the Aotidae, Atelidae, Cebidae, Callitrichidae and the Pitheciidae (Rylands and Mittermeier, 2009).

Platyrrhines split from the other simians in Africa approximately 40-44 million years ago (Schrago and Russo, 2003; Kumar et al., 2017), after which they then crossed the ocean to reach the Americas, where they diversified into the many shapes and sizes we see today. In size, like the lemurs of Madagascar, the platyrrhines vary widely, from the smallest species of ~100g, to the largest of ~9kg (Smith and Jungers, 1997). Unlike the lemurs however, a large degree of variety in sexual size dimorphism is exhibited by platyrrhines, from a lack of dimorphism, or in some cases females being marginally the larger sex, to species such as the Capuchin monkeys, who display a relatively large degree of sexual size dimorphism, with males in some species 50% larger than females (Smith and Jungers, 1997). This range of both size and sexual size dimorphism is perhaps representative of the range of mating systems the platyrrhines have evolved to adopt over the millions of years since arriving in the Americas (Dunbar, 1995).

1.3.4. Catarrhines

The extant catarrhines consist of the Cercopithecidae and the Hominoids (Apes). The Cercopithecidae with twenty-four genera, are the largest of all primate families, and can be divided further into the Cercopithecinae and the Colobinae. Thought to have split somewhere between 16 and 20 million years ago (Kumar et al., 2017), the Colobinae are primarily found in Eastern Africa and Asia, and the Cercopithecinae principally in sub-Saharan Africa, with only the macaques more widely distributed, being found in Northern Africa, throughout Asia and in Gibraltar (Jablonski et al., 2000; Elton and Dunn, 2020).

The Cercopithecidae are typically a large family of primate, with the smallest being the talapoin, a little over 1kg. However, this species is by some margin the smallest of extant species, with the largest, the mandrill, reaching sizes in excess of 30kg (Smith and Jungers, 1997; Elton and Dunn, 2020). As is in the lemurs, the Cercopithecidae fossil record also shows extinct forms as having been considerably larger than even the largest of extant species, with males in the

extinct *Theropithecus oswaldi* projected to have reached sizes as large as 72kg (Delson et al., 2000).

Almost all Cercopithedae, with only few exceptions, exhibit sexual size dimorphism, with males considerably larger than females in several species. This widespread sexual size dimorphism is perhaps representative of the polygynous and polygynandrous mating systems that pervade the family (Rowe and Myers, 2017; Elton and Dunn, 2020).

The apes comprise the small apes (gibbons and siamangs), and the great apes: orangutans, chimpanzees, gorillas and humans. The apes split from the other catarrhines somewhere between 25 and 30 million years ago, with the gibbons splitting from the great apes approximately 20 million years ago (Kumar et al., 2017). The gibbons are considerably smaller than the other apes and are even relatively small when compared to many Old-World monkeys. Gibbons are also unique amongst apes, and rare amongst catarrhines, in that they lack sexual size dimorphism, perhaps a result of the monogamous mating system they have evolved to adopt (Brockelman, 2009).

The great apes are the largest of all extant primates. The largest, the gorillas, reach sizes of up to 170kg. Again, the fossil record evidences even larger species having once lived, with the famous *Gigantopithecus* thought to have weighed up to as much as 500kg (Jin et al., 2009). The great apes also display high levels of sexual size dimorphism along with their large size, as male gorillas and orangutans weigh more than twice that of their female conspecifics (Rowe and Myers, 2017).

Thus, it is apparent that primates have a long and rich history over which they have diversified into the many distinct forms we see today, as well as those the fossil record alludes to. This evolutionary history provides an opportunity to better understand the processes that characterize the evolution of body size and the ways in which these processes differ between males and females.

1.4.   Hypotheses and predictions

The large variation in body size between primate species is reflected in evolutionary rates, with some lineages having undergone more accelerated rates than others(Venditti et al., 2011; Elton and Dunn, 2020). Evolutionary rates also differ between the sexes in cercopithecids, when male rates are compared with females (Elton and Dunn, 2020). Accordingly, it would be expected that rates will differ between the sexes in other lineages in which sexual size dimorphism is also observed.

The phylogenetic comparative methods that will be used enable evolutionary rates to vary from those expected under a Brownian motion model of evolution. Where these rates are accelerated above a value of 1, this indicates active selection has taken place, as more passive forms of evolution, such as genetic drift are less likely to cause rate changes above that expected under Brownian motion evolution. By estimating rates of body size evolution for both males and females, we should be able to identify branch-wise differences in rate between the sexes (Venditti et al., 2011). Such instances in which one sex has undergone significantly accelerated rates over the other are indicative of more intense selection acting upon the branch in question. Branches on which rates differ significantly between the sexes can be attributed to sexual selection, whereby active selection has been far more intense upon only one sex (Cooney et al., 2020) It is possible that I will see accelerated rates in both sexes even in instances that can be attributed to sexual selection, owing to positive genetic correlation. For example, if a species has been subject to intense sexual selection for increased male size, we would expect to see a highly accelerated branch leading to that species in the male phylogeny. But we may also expect to see an accelerated branch in the female phylogeny as the females will likely have increased in size because of genetic correlation. However, it is also possible that genetic correlation, being a relatively weak force compared to active selection, may not return accelerated rates above that expected under Brownian motion. It is important to note that where branches are not accelerated, this does not mean that body size has not increased in these lineages. If sexual size dimorphism is the result of sexual selection, we should see significantly accelerated male rates, but not, or to a far lesser degree, female rates, on branches leading to size dimorphic species. If sexual size dimorphism is primarily the result of natural selection pressures however, with increased size being selected for in

both sexes, but constraints on female size preventing the same degree of size increase as in males, we would expect to see both branches returning elevated rates, with the difference between both less exaggerated as in the example given above. Alternatively, if sexual size dimorphism is due to fecundity selection selecting for smaller females, as has also been previously predicted (Martin et al., 1994; Cassini, 2017), we would expect to see accelerated rates of evolution on the female phylogeny, as branches have undergone active selection for reduced size, whereas no such selection should be present in males.

Given the multitude of factors that are thought to influence body size evolution, I hypothesise that all three of these mechanisms may be present across the primate phylogeny, with no one form of selection being solely responsible for sexual size dimorphism in primates. However, in line with the findings and predictions of Lindenfors et al., (1998) and others, we predict that the most extreme instances of sexual size dimorphism, as those seen in catarrhines and in some platyrrhines, will be the result of sexual selection, with evolutionary rate increases reflecting the intensity of the sexual selection on the male phylogeny, but not so on females.

Mating system has previously been demonstrated to associate significantly with sexual size dimorphism in primates (Kappeler, 1990; Lindenfors, 1998; Cassini, 2020), with findings that mating systems thought to encourage higher amounts of male-male competition and therefore greater sexual selection correlating with higher degrees of sexual size dimorphism (Gordon, 2006; Plavcan, 2012). Such findings lend support to the role of sexual selection in the evolution of sexual size dimorphism, and as such I'll be using mating system as a covariate, representing a proxy for sexual selection in phylogenetic regressions testing male size against female size. Conversely, a number of natural selection pressures are considered to influence size evolution in primates, including terrestriality. Many terrestrial species are larger than their arboreal counterparts. This is thought to be because there is less restraint on body size without the need to navigate through the canopies. Terrestrial species also tend to live in larger groups, this may have an impact on the intensity of sexual selection as there is more competition between males for access to females (Milton and May, 1976; Clutton-Brock and Harvey, 1977; Lindenfors, 1998; Rowe and Myers, 2017). Thus, terrestriality will also be used as a covariate in phylogenetic regression models as a proxy for natural

selection. If sexual selection plays a key role in the evolution of sexual size dimorphism as I am predicting, I expect to see a significant effect of mating system on male size relative to female size, with the highest levels of sexual size dimorphism observed in polygynous and polygynandrous species.

The methods used in Baker et al., (2015) to determine long term trends compatible with Cope's rule from extant data, will be used in this study to compare and contrast male and female evolutionary trends in regard to body size in primates for the first time to my knowledge (Baker et al., 2015). With varying rates demonstrated and expected between the sexes (Elton and Dunn, 2020), the degree to which males and females concord with Cope's rule may also differ. If this is the case, then Rensch's rule would necessarily follow as a consequence of the differential trends for increased size. If sexual selection for increased male size is the driving mechanism behind the observed trend of Cope's rule in haplorrhine primates, as predicted by McClain (1993) and Lindenfors et al., (1998), I should be able to demonstrate a long-term trend in male haplorrhines towards increasing size, but the same trend in female haplorrhines, if present at all should be to a far lesser degree. In addition, given the lack of sexual size dimorphism in strepsirrhine primates, and therefore the lack of sexual selection for larger size, I expect not to find a trend in agreement with Cope's rule in the strepsirrhine lineage in either sex. Such findings would be significant in indicating sexual selection as the primary driving force behind Cope's rule, and consequently Rensch's rule, as a trend towards increased size in males would also indicate a pattern of increased dimorphism if the same trend is not observed in females.

2. Methods

2.1.   Phylogeny

A consensus ultrametric phylogenetic tree of primates was collected and downloaded from TimeTree of Life (TTOL) (Kumar et al., 2017), and converted from Newick to Nexus format using TreeGraph 2.0 (http://treegraph.bioinfweb.info/) (Stover and Muller, 2010). This tree was used for all analyses. A consensus tree was chosen as this was considered to be more suitable for phylogenetic comparative models such as that used in this thesis.

2.2. Data collection

2.2.1. Body mass

The primate body mass data used in this thesis are shown in the appendix section. Smith and Jungers (1997) and Rowe and Myers (2017) were the main sources of body mass data for the primate species included in the analyses, of which there are 289 for which body mass data for both males and females were available. Where data on particular species was absent in these two main references, supplementary sources as detailed in the appendix were sought.

Included in the 289 species for which body mass data were collected, are 128 catarrhines, 77 platyrrhines, 77 strepsirrhines and 7 tarsiers. Only species for which data on both males and females was available separately were included, and species for which only data based on captive animals was available were not included, because of the tendency for captive animals to be larger than their wild counterparts. Where Rowe and Myers (2017) were used, data was taken from that with the highest sample numbers, and all data was for adults only. Species for which body mass data was not collected were removed from the phylogenetic tree, and body masses were log transformed to base 10 prior to analyses. It should be noted that whilst I endeavored to ensure that body mass data was taken from those with the highest sample numbers, several species from both Smith and Jungers (1997) and Rowe and Myers (2017) are represented by small sample sizes. A decision was made to include the maximum amount of species possible as opposed to excluding these species.

2.2.2. Mating system

Mating system data for 270 species were collected from the literature as detailed in the appendix. Species were categorized as being either monogamous, polyandrous, polygynous or polygynandrous. Rowe and Myers (2017) was used to collect mating system data. Many primate species exhibit multiple mating systems depending on a number of factors, such as group size and resource availability (Kappeler, 1990). However, this has not been accounted for here, and in cases

where multiple mating systems are cited, the source with the highest sample number was selected.

2.2.3. Terrestriality

Data was also collected on terrestriality for 287 species, detailed in appendix. These data were taken from Gallen-Acedo et al., (2019), in which species were categorized as being arboreal, terrestrial or both. Gallen-Acedo et al., (2019) compiled data taken from 1,216 studies published between 1941 and 2018, and term what I am referring to as terrestriality as locomotion type. Species were denoted a category based on the main way in which an animal moves in its environment. Arboreal includes species that are strictly arboreal, very rarely going to ground. Terrestrial includes species that carry out the majority of their daily activity on the ground. Species categorized as both includes those which are commonly active on both the ground and in the trees (Gallen-Acedo et al., 2019). Although this is a simple categorization, I consider it to be adequate for the analyses here.

2.3.   Data analyses

2.3.1. Variable traits model of trait evolution

To quantify rates of body mass evolution I used the Bayesian reversible-jump variable rates model of trait evolution implemented in BayesTraits V3 (Meade and Pagel, 2017). The variable rates model allows branch lengths of a phylogenetic tree to be rescaled according to the rate of trait evolution by returning a posterior distribution of rate scalars *(r)* for each branch of a tree, detecting significant shifts in evolutionary rates from an underlying Brownian motion model of evolution. The model allows the detection of rate shifts without prior knowledge or specification of where and when they occur (Venditti et al., 2011).

To determine rates of evolution for each branch of the tree separately for males and females I ran the variable rates model in a Bayesian Markov Chain Monte Carlo (MCMC) framework for male and female log transformed body masses independently. These analyses returned a set of rate scalars for each branch, where an *r* of >1 implies an increased rate of evolution when compared to the background rate, and an *r* of <1 a decreased rate. The median rate scalars for each branchfrom each model, taken from the variable rates post-processing tool (available at www.evolution.reading.ac.uk/VarRatesWebPP), were used to rescale branches on the phylogenetic tree, stretching branches that have undergone increased rates, and compressing those that have undergone decreased rates. Two separate trees were created: one with branches rescaled to male median rate scalars, and one with branches rescaled to female median rate scalars (Meade and Pagel, 2017). The rescaled trees were also used to estimate ancestral states of body mass at each node for both males and females in order to determine direction of selection.

Default priors (a gamma prior on each rate parameter with parameter α = 1.1 and parameter β rescaled such that the median of the distribution is 1, thus ensuring that an even number of rate increases and rate decreases are proposed (Venditti et al., 2011)) were used on the MCMC chains, and each repetition was run with 1 billion iterations, with the first 250 million removed as burn in. Each model was run three times and convergence of the chains was confirmed using Tracer and the R package *coda* (Plummer et al., 2006). Median rate scalars used to rescale the branches of the tree were taken from the first run. Log marginal likelihoods were estimated using a stepping-stone sampler. The stepping-stone sampler estimates the marginal likelihood by placing a number of 'stones' which link the posterior with the prior, the stones are successively heated, forcing the chain from the posterior towards the prior, providing an effective estimate of the marginal likelihood (Meade and Pagel, 2017). The marginal likelihoods from the stepping-stone sampler are expressed on a natural log scale, and these values can then be converted into Log Bayes Factors, which are used to test for statistical difference between models (Meade and Pagel, 2017).

2.3.2. Determining rate shifts

To determine rate shifts in body mass evolution of one sex over the other, I took the median rate scalars from the independent variable rates models and log transformed them (Venditti, 2011). Rate scalars were log transformed as median rate scalars are estimated from zero to infinity. So, in a regression, the intercept could go below zero, which is not very appropriate as we know y and x cannot fall below zero. However, this cannot happen when the scalars have been logged. Thus, the results from the transformed analyses are biologically interpretable, whereas non-transformed scalars may not be. I then calculated the difference between the rates for each corresponding branch of the tree (male logged median r – female logged median r). This allowed me to calculate the difference in evolutionary rate between males and females for each branch – where a difference of 0 is equal to a branch evolving at the same rate in both sexes – detecting rate shifts that lead to changes in sexual size dimorphism.

Instances in which one sex has undergone accelerated rates ($r = >1$), but the other has not ($r = 1$) may suggest sexual or fecundity selection. Such cases may still lead to changes in sexual size dimorphism if the r values differ however, this may be representative of heavier constraints placed upon one sex, preventing equal evolution.

By calculating the difference between males and females for each branch on the tree, I was also able to determine branches in which the disparity of selection strength has been the strongest (branches with the greater difference between male and female median rate scalars), therefore identifying likely instances of more intense sexual selection.

2.3.3. Path-wise rates

Path-wise rates are the sum of all rate-scaled branches (Original branch length as measured by time, multiplied by the median rate scalar) leading from the root to the tip of the phylogenetic tree. These rates account for the total change in body mass a species has experienced throughout its evolution and allow for the

detection of long-term evolutionary trends (Baker et al., 2015). I calculated path-wise rates of evolution for both males and females in all 289 species included in these analyses.

2.3.4. Male path-wise rate vs female path-wise rate: correlated evolution

A phylogenetic generalized least squares (GLS) regression model was used to plot the relationship between path-wise rates of males and females. Female path-wise rate was used as the independent variable and male path-wise rate as the dependent variable. This regression enabled me to determine the correlation between male and female evolutionary rates.

A separate-slopes model was used to determine the different relationships between male and female evolution across clades; strepsirrhines, platyrrhines, catarrhines and tarsiers (Baker et al., 2015). The separate-slopes model allows for the observation of instances where rates differ both between the sexes and within each sex, by identifying clades with elevated rates. To allow for the separate-slopes model, each species was assigned to the group in which it belongs using standard contrast coding ("dummy coding"). This model estimates both the intercept and slope for each assigned group.

For both slopes and intercepts the proportion of the posterior distribution of each regression parameter that was more than zero was determined. If the value of p is <0.05, this means that less than 2.5% of the posterior distribution was more than zero. In this case, I consider such a parameter to be significantly different from zero. In order to compare slopes and intercepts of each group included in the separate-slopes models, I calculated the difference between each pair of groups at each iteration, again calculating the proportion of these distributions that were greater than zero. If p is <0.05 I consider the slopes/intercepts to be significantly different from one another (Baker et al., 2015).

Where slopes do not significantly differ between groups, using the measurement of significance detailed above, a model in which only separate intercepts are estimated for each group is preferred.

2.3.5. Path-wise rates vs body mass: Determining directional trends in the evolution of primate body mass

Regression models using path-wise rate as the independent variable and $\log^{10}$ body mass as the dependent variable were also run using phylogenetic GLS, with separate models for males and females. These models allow the identification of directional trends, such as Cope's rule, in respect to the evolution of body mass. If a directional trend has taken place over the course of primate evolution, an association between path-wise rate and body mass will be evident. This association will be positive if there is a tendency for increased evolutionary rates to lead to larger size (Cope's rule), or negative if the tendency is for increased rates to lead to reduced size. A positive association would indicate that where active selection for body mass has occurred (branches in which $r = >1$), it has more often been for larger size (Baker et al., 2015).

By running independent models of body mass against path-wise rate for both males and females, I am able to determine whether evolutionary trends differ between the sexes. If sexual selection for increased size in males has taken place throughout the evolution of primates, resulting in male-biased sexual size dimorphism, a directional trend will be present in male body mass evolution, but not so in female.

Given the variation seen in body mass and sexual size dimorphism of extant species, it is likely that the association between path-wise rate and body mass may differ between primate families, and so as before, I also ran a separate-slopes variation of both models, allowing slopes and intercepts to differ between the primate groups specified above: strepsirrhines, platyrrhines, catarrhines and tarsiers. Each species in the separate slopes models were assigned to the group in which they belong using standard contrast coding.

Again, p values were determined by the proportion of the posterior distribution of each regression parameter that was more than zero, for both intercepts and slopes between groups. If slopes were found to not significantly differ (a p value of >0.05), a model in which only separate intercepts were estimated was preferred.

2.3.6. Determining effects of mating system and terrestriality

To determine whether differences in evolutionary rate between males and females could be explained by covariates, we used mating system as a proxy of sexual selection and terrestriality as a proxy of natural selection. I applied the variable rates model in a phylogenetic regression framework, first with male body mass as the dependent variable, female body mass as the independent variable and mating system as a covariate. This allowed me to estimate the rate of male body mass evolution relative to female body mass evolution whilst accounting for mating system.

Each species was assigned to the appropriate mating system (monogamous, polyandrous, polygynous, polygynandrous) using standard contrast coding. I also ran a separate slopes model, allowing the slopes to differ between mating systems as well as the intercept. BayesTraits automatically removes species for which no data is entered in the input files, and so therefore species lacking mating system data are not included in the analyses.

As in previous models, a measure of significance was determined by the proportion of the posterior distribution of each regression parameter that was more than zero. If less than 2.5% was found to be more than zero, such a parameter was considered significantly different from zero. To compare slopes and intercepts of each mating system, I calculated the difference between each pair of mating systems at each iteration, again calculating the proportion of these distributions passing zero, if less than 2.5% , the slopes/intercepts are considered to be significantly different from one another. Also as in previous models, if the slopes in the separate slopes model were found to not significantly differ between mating systems, we prefer the model in which only separate intercepts are estimated.

It should be noted that there is evidence in the literature that the association between mating system and sexual size dimorphism differs between clades (Kappeler and van Schaik, 2002; Gordon, 2006). Several authors have shown that no association exists between mating system and sexual size dimorphism in

lemuriforms, but that there is an association in catarrhines and platyrrhines, with the catarrhine pattern being considerably stronger than the platyrrhine pattern (Kappeler and van Schaik, 2002; Gordon, 2006; Cassini, 2020). Given this evidence it is possible that the primate wide analyses performed in this study may conflate these clade differences, and this should be considered when interpreting and discussing the results.

BayesTraits removes species for which no terrestriality data was entered, and so such species are not included in the analysis.

For each analysis detailed above, I sampled every 50,000 of 500,000,000 iterations, with the first 500,000 removed as burn in. Each model was run three times and convergence of the chains confirmed using Tracer and *coda* (Plummer et al., 2006). Log marginal likelihoods were estimated using a stepping-stone sampler (Meade and Pagel, 2017).

2.3.7. Model comparison

In all MCMC models run during the above analyses, rate heterogeneity as determined by the variable rates models was tested for statistical significance using the Bayes Factor (BF). Homogenous Brownian motion models were run as the simpler alternative to the variable rates models, and log BF calculated (2[log marginal likelihood variable rates model – log marginal likelihood Brownian motion model]). A log BF of >2 is considered positive evidence for the complex model (variable rates model) (Meade and Pagel, 2017).

3. Results

3.1.   Model Comparison

The log marginal likelihood for the male models were 94.16952833 for the variable rates model (complex model), and 80.217881 for the null model (simple model). Using the formula: Log Bayes Factors = 2(log marginal likelihood complex model – log marginal likelihood simple model), the log bayes factor was 27.903.

For the female models, the log marginal likelihood for the variable rates model was 100.388159 and for the null model 91.645512. Using the same formula as above, the bayes factor was 17.485294.

A log bayes factor >10 indicated very strong evidence in favour of the complex model, in this case the variable rates model, as the best fitting model over the null model, which in this case was a Brownian motion model. Therefore, the variable

rates model is a better fit than the Brownian motion model in both males and females for this data set.

3.2.   Male body mass evolutionary rates

Of 560 branches in the primate phylogeny included here, 228 had rescaled median rate scalars in males (41%). Of those rescaled, 117 (51%) were >1, meaning these branches underwent accelerated evolution above that of the background rate, whereas 111 (49%) were <1 (slower rates than expected) (Figure 1a). See Table 1 for the 10 highest rate scalars in the male model.

3.3.   Female body mass evolutionary rates

The variable rates model of female body mass evolution returned rescaled median rate scalars on 102 branches of the 560 total branches included in the phylogeny (18%). Of those rescaled, 95 had median rate scalars >1 (93%), and 7 rate scalars <1 (7%) (Figure 1b). See Table 2 for the 10 highest rate scalars in the female model.

Table 1 Ten highest resulting median rate scalars from the variable rates model of male body mass evolution.

Ten highest rate scalars on male tree			
Median rate scalar	**Branch leading to**	**Clade**	**Direction**
25.25729	Hominids	Catarrhine	Increase
11.00260	Atelidae	Platyrrhine	Increase
8.333782	*Callithrix pygmaea*	Platyrrhine	Decrease
7.800376	*Callithrix humilis*	Platyrrhine	Decrease
6.665999	*Miopithecus talapoin*	Catarrhine	Decrease
5.919733	*Nasalis larvatus*	Catarrhine	Increase
5.579183	*Mandrillus sphinx*	Catarrhine	Increase
5.140523	Catarrhines	Catarrhine	Increase
4.616103	Mandrillus	Catarrhine	Increase

| 3.753284 | *Macaca nigrescens* | Catarrhine | Decrease |

The higher the rate scalar the faster the rate of body mass evolution on the corresponding branch of the tree. Seven of the ten highest were observed in the catarrhine family.

Table 2 Ten highest resulting median rate scalars from the variable rates model of fe body mass evolution.

Ten highest rate scalars on female tree			
Median rate scalar	**Branch leading to**	**Clade**	**Direction**
15.328713	Hominids	Catarrhine	Increase
13.118142	Atelidae	Platyrrhine	Increase
9.892585	*Callithrix pygmaea*	Platyrrhine	Decrease
6.638668	*Callithrix humilis*	Platyrrhine	Decrease
6.470272	*Macaca ochreata*	Catarrhine	Decrease
5.225157	*Miopithecus talapoin*	Catarrhine	Decrease
4.388696	Mandrillus	Catarrhine	Increase
4.00906	*Semnopithecus hector*	Catarrhine	Increase
3.944972	*Macaca arctoides, Macaca assamensis, Macaca thibetana*	Catarrhine	Increase
3.917561	*Macaca thibetana*	Catarrhine	Increase

The four highest rates are on the same branches as the four highest rates on the male tree, and as on the male tree, seven of the ten highest are in the catarrhine family. However, not on the branch leading to the catarrhines.

3.4. Sexual dimorphism

Of the 560 total branches on the tree, 305 saw no difference in rates between males and females (54%). 169 branches had a negative difference (30%), and 86 a positive difference (16%) (Figure 2). 111 (66%) of the negative difference branches were the result of rate scalars <1 in male platyrrhines, suggesting that in these cases females had not undergone accelerated evolution, but rather males had undergone slower than expected evolution. None of the 86 positive differences were the result of rate scalars <1 in either males or females, suggesting that in all instances males had undergone accelerated evolution and females had either not undergone any accelerated evolution over that expected, or had done so, but to a lesser extent than males.

3.5. Clade-specific results

3.5.1. Catarrhines

Amongst the male catarrhines, 79 branches were rescaled of the 247 total branches (32%). Of these, 72 (91%) showed accelerated rates (median rate scalar >1), and 7 (9%) decelerated (median rate scalar <1). 7 of the 10 highest rate scalars of the primate phylogeny occurred within this family, with the highest occurring on the branch leading to the hominids (Table 1). The branch leading to all catarrhines underwent the eighth highest rate increase (Table 1). This suggests that male catarrhines, at their root, underwent a rapid burst of body mass evolution, resulting in larger size.

Of the 247 branches amongst the female catarrhines, 50 median rate scalars were rescaled (20%). Of these, 43 (86%) showed accelerated rates (>1), and 7 (14%) decelerated rates (<1). 7 of the 10 highest rate scalars of the female primate phylogeny occurred within the catarrhines (Table 2).

Of the 247 catarrhine branches, the difference between male and female rate scalar was 0 (no difference) in 165 (67%), positive, meaning males underwent higher rates of evolution than females, in 60 (24%), and negative, meaning the reverse, in 22 (9%). The branch showing the largest difference is the branch leading to *Nasalis larvatus*. The second largest difference is seen on the branch leading to *Mandrillus sphinx.* The next largest difference is seen at the root of all catarrhines. Males underwent a rapid burst of body mass evolution on this branch, whereas females did not (Figure 1).

3.5.2. Platyrrhines

Amongst male platyrrhines, 123 branches from 153 total branches saw rescaled median rate scalars (80%). Of these, the vast majority were decelerated, with 105 (85%) returning rates <1, and 18 (15%) rates >1. However, despite the average

rate scalar being <1, some branches did see considerably accelerated rates, with 3 of the 4 highest rate scalars occurring amongst the platyrrhines (Table 1).

Amongst female platyrrhines, only 3 branches were rescaled of the 153 total branches in this group (2%). All 3 of these had median rates >1 (Table 2).

Of the 153 platyrrhine branches, in only 28 branches was the difference 0 (18%). 17 were positive (11%), and 106 negative (69%). Of the 106 negative difference branches, 104 (98%) are the result of median rate scalars <1 in the male model, in which the equivalent female branches underwent no change in rate from the background rate. Of the positive difference branches, the largest difference is seen on the branch leading to the capuchin monkeys (Figure 2).

3.5.3. Strepsirrhines

Among male strepsirrhines, of 149 branches, 26 were rescaled (17%). All 26 rescaled branches showed accelerated rates of evolution.

Among female strepsirrhines, 49 were rescaled (33%). In all these rescaled branches the median rate scalar was >1, indicating accelerated evolution.

Among strepsirrhines, 99 of the 149 total branches showed no difference between male and female median rate scalars (66%). 41 branches showed a negative difference (28%), and 9 a positive difference (6%) (Figure 2).

3.5.4. Tarsiers

No branches were rescaled within the tarsiers for either sex.
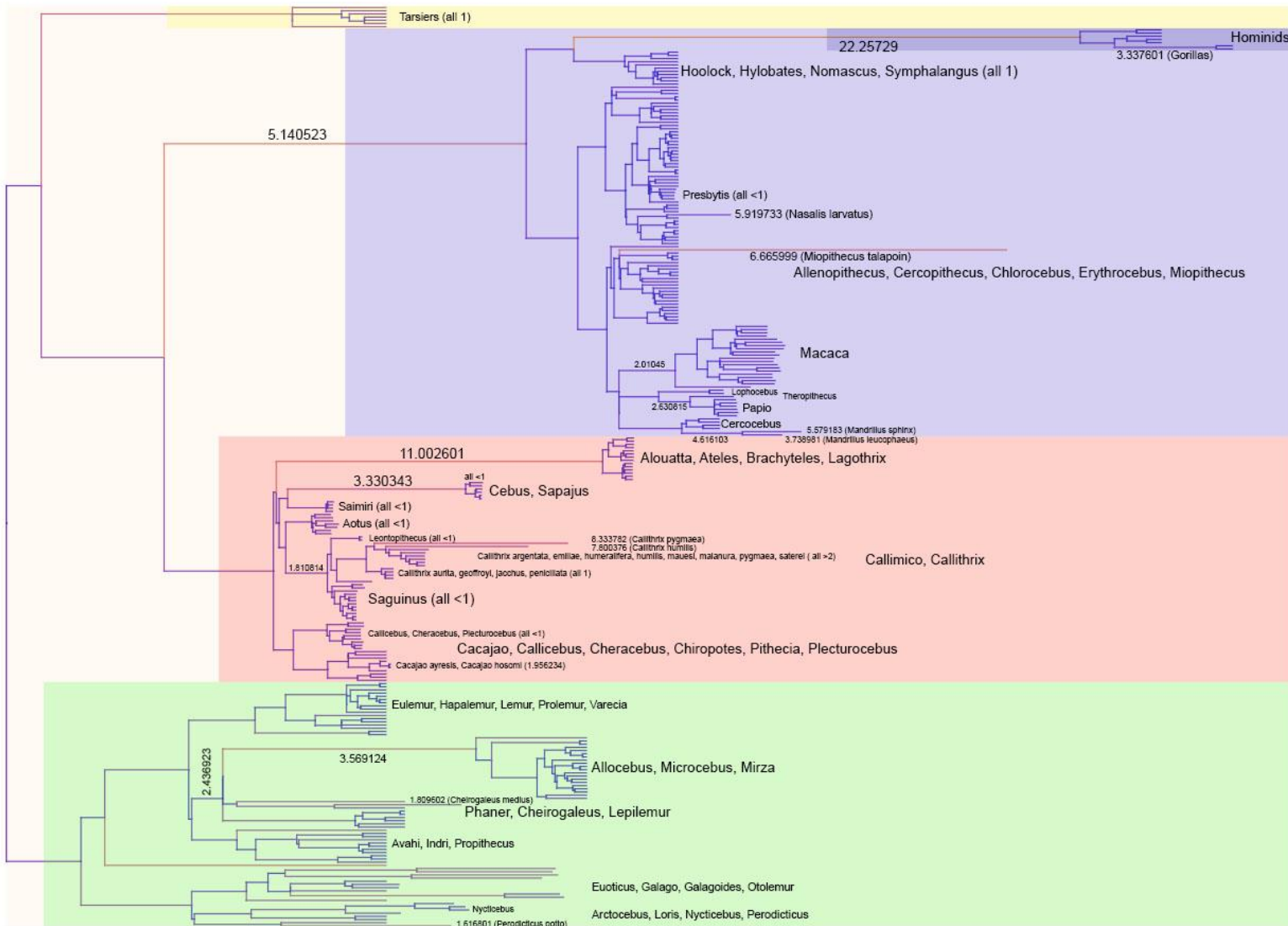
Figure 1 Rescaled primate phylogenetic tree

a) Male phylogeny

Primate phylogenetic tree, with branches rescaled to the median rate scalars taken from the variable rates model of male body mass evolution. Stretched branches represent branches that have undergone accelerated evolution, compressed branches represent branches that have undergone slower evolution than would be expected under a Brownian motion model. Branches are also coloured according to rate of evolution, with branches moving from blue to orange the more they are stretched. Background colours indicate family; yellow = tarsiers, blue = catarrhines, red = platyrrhines, green = strepsirrhines.

b)   Female phylogeny
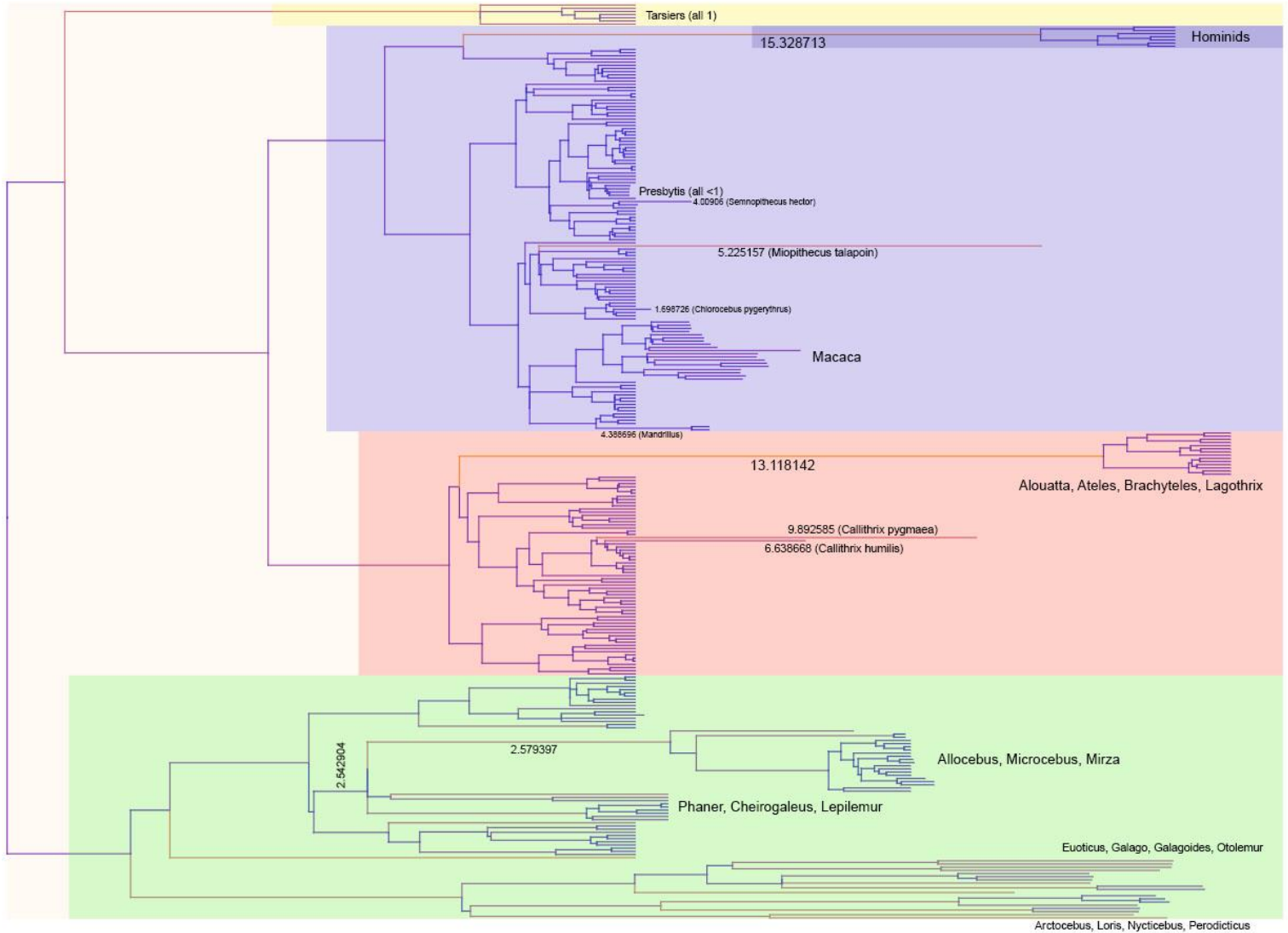
Primate phylogenetic tree with branches rescaled to the median rate scalars taken from the variable rates model of female body mass evolution. Branches are stretched or compressed to represent accelerated or slower evolution than expected under a Brownian motion model. Branches are also coloured according to rate of evolution, with branches becoming more orange the more stretched they are. Background colours indicate family; yellow = tarsiers, blue = catarrhines, red = platyrrhines, green = strepsirrhines.

Figure 2 Histogram showing the differences between male and female rate scalars

Histogram showing the differences between male and female rates (male median rate scalar –
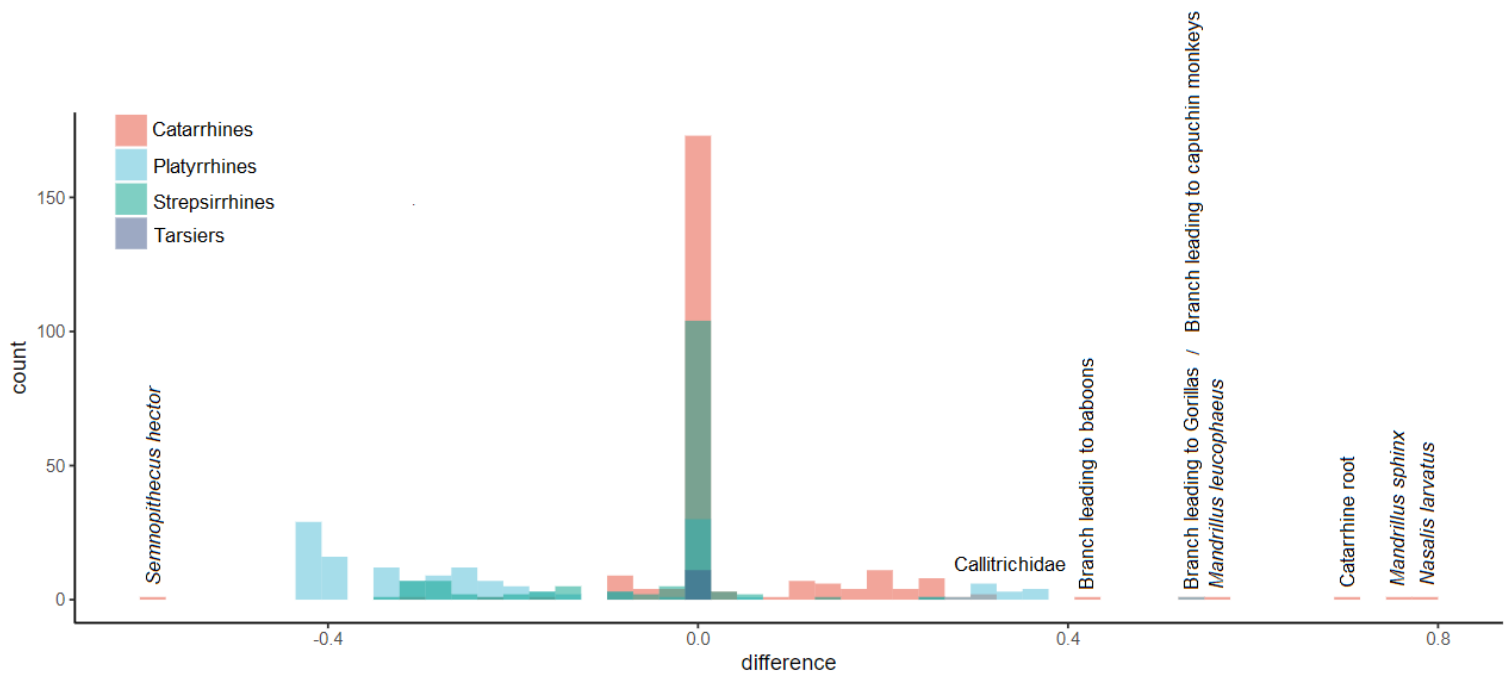
female median rate scalar). A difference of 0 indicates no difference, a positive difference indicates instances in which males have undergone elevated evolutionary rates compared to females, and a negative difference indicates instances in which females have undergone elevated rates relative to males. The majority of branches showed no difference (54%), 30% showed a negative difference and 16% a positive. The largest differences were seen in catarrhine branches, most notable on the branches leading to *Nasalis larvatus* (0.772302) and *Mandrillus sphinx* (0.746571). Interestingly the next highest difference was observed on the branch leading to all catarrhines (0.711007). Indicating that the heightened sexual size dimorphism observed in catarrhines is largely the result of a rapid burst of male body mass evolution, most likely due to sexual selection for increased male size, that went on to define the entire clade.

3.6.   Male path-wise rate vs female path-wise rate

No significant difference between the slopes of each family was found, and so results are taken from a model only estimating separate intercepts. No significant difference was found between the intercepts of strepsirrhines and platyrrhines, however, significant differences were found between catarrhines and strepsirrhines ($p = {<}0.05$), as well as between catarrhines and platyrrhines ($p = 0.05$). The intercept of male path-wise rate against female path-wise rate was significantly higher than the intercepts of platyrrhines and strepsirrhines (tarsiers were not included in the analysis due to no rate heterogeneity being found between males and females). The higher intercept in catarrhines is reflective of higher

evolutionary rates in male catarrhines than in females. Intercepts for all three families differ significantly from zero.

3.7. Path-wise rates vs body mass

3.7.1. Males

When comparing path-wise rates with body mass a positive slope indicates that instances in which accelerated rates of evolution have occurred, they have more often than not been in the direction of increased size. A negative slope indicates the opposite, that accelerated rates of evolution have more often been in the direction of decreased size.

I found significant differences between slopes of path-wise rate against body mass in the primate families, and so results are taken from the separate-slopes model. The slope from strepsirrhines significantly differs from catarrhines, but not so from platyrrhines. The slope between platyrrhines and catarrhines is also significantly different. Tarsiers were not included in the analysis.

Catarrhines show a significantly positive slope between path-wise rate and body mass ($p = <0.05$). Strepsirrhines show a significant negative slope between path-wise rate and body mass ($p = <0.05$). The slope in platyrrhines does not differ significantly from zero (Figure 3a). These results suggest that in male catarrhines there is a directional trend towards increasing size over time. No such trend is present in male platyrrhines, and the opposite trend, directional evolution towards smaller size, in strepsirrhines.

3.7.2. Females

As in males, slopes significantly differed between primate families and so results are taken from the separate-slopes model. I find a significant difference in slope between strepsirrhines and platyrrhines, strepsirrhines and catarrhines, but not so between platyrrhines and catarrhines. Tarsiers were not included in the analysis.

Strepsirrhines show a significant negative slope between path-wise rate and body mass (p = <0.05). The slope in neither catarrhines nor platyrrhines differs significantly from zero (Figure 3b).

Figure 3 Path-wise rates regressed against body mass

a) Males   b) Females

Path-wise rates regressed against body mass in **a)** males, and **b)** females. Dotted lines indicate slopes not significantly different from zero. Male catarrhines show a significant positive slope, whereas female catarrhines do not. Strepsirrhines show a significant negative slope in both sexes.

3.8. Mating system

Slopes didn't differ between mating systems and so results are taken from the model estimating separate intercepts only. I find a significantly higher interceptin polygynandrous species when compared to polyandrous and monogamous species, when comparing male evolutionary rates against female evolutionary rates accounting for mating system. I also find a significantly higher intercept in polygynous species than in polyandrous species. Pair-wise comparisons between polygynous species and monogamous species do not show a significant difference, although it is not far from being significant (p = 0.073). No significant difference in intercept was found between monogamous and polyandrous species, and neither between polygynous and polygynandrous species. The intercepts for both polygynous and polygynandrous species significantly differ from zero, monogamous and polyandrous intercepts do not.

3.9. Terrestriality

44

I find no significant difference in slopes or intercepts in all pair-wise comparisons between terrestriality types.

4. Discussion

4.1.   Summary of main findings

Most previous studies looking at evolution of body mass and sexual size dimorphism have largely relied upon models determining physiological, morphological, ecological and behavioural correlates of variation in trait values among extant, and in some cases extinct, species (Plavcan and Van Schaik, 1991; Cassini, 2017; Cassini, 2020; Smith and Cheverud, 2002; Gordon, 2006). Whilst providing insight into the potential selection pressures that give rise to changes in both body mass and sexual size dimorphism, these methods are limited in what they can tell us about the evolutionary history of species and the relative roles played by sexual and natural selection. By using more recent comparative methods to analyse the evolutionary history and patterns of male and female primates independently, it is possible to disentangle sexual selection and natural selection by identifying instances in which males and females have undergone either shared selection, or instances in which there is a difference in rate between the sexes. This method also allowed the detection of long-term evolutionary trends in both sexes separately, consequently allowing me to determine the influences of natural selection and sexual selection in the evolution of sexual size dimorphism, as well as on the observation of Cope's rule and Rensch's rule.

The results of this study show it is clear that no one pattern explains the evolution of body mass and sexual size dimorphism in primates; different clades show different patterns. Both between and within clades, individual branches on the phylogeny have been subject to strong selection, both sexual and natural. Both processes can lead to changes in overall body mass as well as in sexual size dimorphism, but I find that the vast majority of cases in which sexual size dimorphism increases significantly, this is the result of selection for larger male size. The most notable instance in which this is the case is of an increased evolutionary rate on the branch leading to male catarrhines, suggesting sexual selection as the leading cause of the heightened sexual size dimorphism within this group.

Furthermore, I find that across all primates, only male catarrhines show a general trend for increasing size through time. Thus, any directional trend towards increased size in primates appears to be the result of sexual selection acting on male body size. A significant consequence of this finding is that of an intrinsic link between Cope's and Rensch's rule. Sexual selection for larger male size is the cause of both, hence, both rules collapse into a single evolutionary trend, in which male size increases both absolutely and relative to females. With this in mind, male catarrhines may have skewed the results of previous studies in which primates were found to follow these rules.

4.2.   Cope's rule and Rensch's rule

The findings of this study support suggestions that the appearance of Cope's rule is explained by sexual selection for larger male size (McLain, 1993; Lindenfors, 1998). It has been postulated that for Cope's rule to exist as a rule, large size must provide a fitness advantage (Hone and Benton, 2005). However, despite the intrinsic advantages large size is thought to bring (Kingsolver and Pfennig, 2004), my results provide no evidence of a trend driven by naturally selected increasing size. Instead, the trend towards increasing average size in catarrhines results from effects solely on male size, consistent with selection on males in intra-specific competition for mating success.

The lack of evidence for Cope's Rule may be because the optimum size of a species is variable and depends highly on a number of ecological factors (Jones and Purvis, 1997). Larger size can also decrease fitness in certain circumstances, particularly when resources are scarce (Hone and Benton, 2005; Baker et al., 2015; McKinney, 1997), whereas when larger male size equates to greater mating success it will always mean higher fitness.

These results suggest possible new interpretations to the patterns observed by Baker et al (2015), who found evidence for a trend for increasing size through time (Cope's rule) in 10 of 11 mammalian orders, including primates (Baker et al, 2015). The authors concluded that these findings almost certainly reflect an adaptive response to new selective circumstances, suggesting competition, climate change

and dietary specialization as potential forces (Baker et al, 2015). However, the study examined only average body size for both sexes, and as a result did not consider different patterns for males and females or sexual selection as a potential driving force. The results of the current study, however, indicate sexual selection and clade-wise differences as being critical in the evolutionary history of species and observation of long-term trends. Consequently, demonstrating how evolutionary explanations for supposed trends and patterns can be overlooked if males and females separately, and by proxy sexual selection are not considered as driving forces.

The debate as to whether primates follow the general pattern of Cope's rule is one that is very much still alive, with recent papers, such as that by Baker et al (2015) cited above, finding evidence in support, and others finding the contrary; no evidence of a directional trend for increasing size (Montgomery et al, 2010). However, this study provides the most in-depth investigation into the question to date and finds the answer to be far more nuanced than may have been thought previously. Patterns of evolution vary widely, but no trend for an intrinsic increase in size with time exists in primates. However, sexual selection for larger male size has driven the observation of such a trend in male catarrhines alone.

The results of this study also support the hypothesis drawn from the suggestion that Cope's and Rensh's rule are linked. I find a trend for increasing size in male catarrhines, but not so in females, and with this comes a trend for increasing sexual size dimorphism. This finding suggests that the observed trend of Cope's rule and Rensch's rule in primates are a side-effect of selection for increased male size. Previous studies have found Rensch's rule to be prominent in certain clades of catarrhines (Cardini and Elton, 2008), and I find an increase in sexual size dimorphism with body mass to be a feature of catarrhines more generally. This corresponds to the interpretation of sexual selection for larger male size as the force behind any observed trend compatible with Rensch's rule; catarrhines are the only group in which I find widespread historical sexual selection.

Elevated rates of evolution in both sexes were found on the branch leading to the hominids. Here, the rate is higher in males than in females. It is likely then that natural selection is behind the increased sizes we see in hominids above that of

monkeys. A higher rate in males however opens up a number of possible explanations. It is possible that along with natural selection, further sexual selection took place early in the evolution of the hominids, and these selective forces have led to not only larger size, but also larger sexual size dimorphism. Another possible explanation is as a result of the disadvantages that large size brings to female mammals (Martin et al., 1994; Cassini, 2017; Elton and Dunn, 2020). This explanation would mean that natural selection may also be capable of leading to a trend compatible with Rensch's rule, as increased sexual size dimorphism comes with increased size due to the countering forces of fecundity selection, as suggested by Cassini, 2017 & 2020. However, I find no other instances to support this, with other examples across the primate phylogeny of elevated rates in both sexes where males haven't undergone the higher rate over females that would be expected if it was the case that when natural selection causes increased size, it does so to a greater extent in males than in females. Therefore, natural selection for larger sizes in both sexes does not necessarily mean that sexual size dimorphism will also increase.

These findings propose interesting questions about the validity of both Cope's and Rensch's as rules. As if it is the case, as I find it to be in primates, that the observation of these trends is due in large part to sexual selection, studies would need to be conducted across a wider range of orders, particularly in the mammals, to test whether the results of this study apply to all groups, and not only to primates. It must be considered that the results of these studies depend upon the accuracy of the model being used. The variable rates model used in this study was chosen because it has been shown to more accurately estimate ancestral states and therefore evolutionary patterns in previous studies, however testing the accuracy of the model with this specific data set was not within the scope of this study, and this must be considered when reflecting on the results. It is also important to note that with any study looking at long term evolutionary trends, the inclusion of reliable fossil data can only improve the accuracy of results, and any study that does not include such data will have its limitations because of this. Fossil data were not included here because of the unavailability of independent body size data for male and female fossil species. Future studies that are able to include fossil data will build upon the results from extant data.

4.3.   Sexual selection as the leading cause of sexual size dimorphism

The finding that increased sexual size dimorphism in primates is most likely the result of sexual selection for increased male size supports the findings of previous studies (Clutton-Brock et al., 1977; Clutton-Brock, 1985; Plavcan and van Schaik, 1997a; Lindenfors, 1998; Plavcan, 1995, 1999, 2001; Gordon, 2006), which have strongly correlated sexual size dimorphism with proxies for sexual selection, notably mating system and male-male competition intensity (Plavcan, 1995; Gordon, 2006). Such correlations suggest large male size is clearly of benefit in competition for mating success, and therefore is sexually selected. My results support the findings from correlational studies by determining in which sex selection has taken place in cases where changes in sexual size dimorphism have occurred. I find that whereby sexual size dimorphism results from multiple varying routes, and that no one mechanism can explain the evolution of variation in size between males and females, the most extreme cases are the result of selection for larger size acting on males; sexual selection. The most notable example of this is seen in catarrhines. The finding that the increased sexual size dimorphism in catarrhines above that of other anthropoids is the result of intense sexual selection for male size is therefore one that places a large emphasis on sexual selection as the leading cause of sexual size dimorphism in primates, with the most extreme cases of sexual size dimorphism having resulted from such selection.

The benefits of the methods used, as well as being able to identify specific branches that have undergone selection, as well as the direction of selection, are that by separating the sexes, sexual size dimorphism is not being measured solely as a function of selection on males, with females acting as a baseline for comparison, as has been the case in many previous studies into sexual size dimorphism (Plavcan, 2001). Instead, I have been able to determine selection on female body size independently. This enables me to identify, or not, multiple mechanisms that have previously been hypothesized to lead to sexual size dimorphism in primates. Such alternative mechanisms to sexual selection have been that of 1) body size generally, notably put forward by Leutenegger and Chevered, 1982. Following from the observation of Rensch's rule, it has been

proposed that sexual size dimorphism will increase as a result of increases in body size overall. However, I find that sexual size dimorphism does not increase intrinsically in instances where body size increases in both sexes. The observation of elevated rates of evolution on certain branches in both sexes without the resulting increase in sexual size dimorphism that would be expected if body size dimorphism increased with size refute this mechanism as a leading cause of sexual size dimorphism. As noted above, it is possible that selection for increased size in both sexes can lead to increase sexual size dimorphism also, as may be the case with the hominids (although not conclusively), but most instances and the most extreme instances of sexual size dimorphism are not the result of increases in overall body size. 2) Fecundity selection and differential responses to natural selection pressures has also been suggested (Cassini, 2017; Cassini, 2020; Martin et al., 1994). The pressures that large size puts on female mammals in terms of reproduction are thought to lead to fecundity selection for smaller sized females, which may in turn lead to sexual size dimorphism (Cassini, 2017; Ralls, 1977). The constraints that fecundity selection places on females may also lead to sexual size dimorphism if the constraints on female size prevent them from reaching the same sizes as males (Martin et al., 1994; Cassini, 2020). I find that this is a possible explanation in apes, but there is no evidence for this being the case elsewhere among primates. There are no instances in which increased sexual size dimorphism results from an elevated rate on a female branch in the direction of reduced size, with no corresponding elevation on a male branch, that would be expected were fecundity selection on females a cause of sexual size dimorphism. aside from the case with hominids, there are not widespread cases of selection on both sexes acting to increase overall size, with selection being stronger in males and consequently leading to increased sexual size dimorphism, that would be seen if natural selection for larger size, with the constraints faced by females limiting female evolution relative to males, were a leading cause of sexual size dimorphism in primates. 3) Correlated response, argued by Greenfield, 1996, is a phenomenon in which traits evolve in both sexes when the gene for said trait is not located on the sex chromosomes (Lande, 1980). Sexual size dimorphism would then result if the trait in question were to be disadvantageous in one sex, in such a case, selection should favor a mechanism that decouples the expression of the trait between males and females (Plavcan, 2001). If this were the case with body mass

in primates, similarly to fecundity selection, it would be evident in the rescaled phylogenies by elevated rates (indicative of selection) on the female branch, in the direction of reduced size, but not so on the corresponding male branch. However, there are no instances of this occurring. 4) Predation defense is another theory that has been suggested as a potential cause of sexual size dimorphism. Predation defense is the suggestion that large size evolves to make a species less susceptible to predation (DeVore and Washburn, 1963; Leutenegger and Kelly, 1977; Plavcan and van Schaik, 1992; Plavcan and van Schaik, 1997). This idea was largely because terrestrial species tend to be larger in size and more sexually dimorphic in size than arboreal species. However, I find no significant effect of terrestriality on sexual size dimorphism, this would seem to refute the suggestion of predation defense as a cause of sexual size dimorphism, as those terrestrial species do not seem to be significantly more dimorphic, despite the assumed increased risk of predation.

It has become considered an oversimplified explanation to view sexual dimorphism as a unitary character resulting from sexual selection (Ralls, 1977, Plavcan, 2001), and this study does not deny the role that other factors have had in the evolution of sexual dimorphism. However, I do find strong evidence for sexual selection being a leading cause of sexual size dimorphism in primates. Instances in which sexual size dimorphism increases drastically, and the most extreme instances of sexual size dimorphism are most likely the result of selection for larger male size, indicated by accelerated rates of evolution above that of Brownian motion and processes that can be considered to fall within this model of evolution.

4.4.   Sexual selection early in catarrhine evolution

I find that not only is the increased sexual size dimorphism in catarrhines the result of sexual selection, but also that this was initiated at the root of all catarrhines, indicated by the elevated rate on the branch leading to the catarrhines on the rescaled male phylogeny. This suggests that the heightened sexual size dimorphism that characterises this group of primates evolved early and rapidly,

forming the baseline sexual size dimorphism we see in catarrhines. Subsequently, a number of branches have undergone further selection, which in the vast majority of cases has occurred in males only, in the direction of increased size, and therefore further increased sexual size dimorphism, as we see in the most extreme instances such as *Nasalis larvatus* and *Mandrillus sphinx.*

Sexual size dimorphism can be difficult to determine from the fossil record, primarily owing to the scarcity of specimens for many extinct species, of which in many cases sex is not possible to determine, or specimens for both sexes of one species may have not yet been discovered (Soligo, 2006; Tavare et al., 2002). However, what evidence there is suggests that sexual size dimorphism is present in the primate fossil record from as far back as the late Eocene (Simons et al., 1999), and is known from early catarrhine specimens. *Aegyptopithecus zeuxis,* a species of propliopithecoid, one of the earliest known catarrhine groups, has sexually dimorphic canines, that along with craniofacial morphology and brain size all suggest that *Aegyptopithecus zeuxis* displayed sexual size dimorphism (Fleagle et al., 1980; Simons et al., 2007). A number of catarrhine specimens dating from the origin of the clade to the present day are also known to have been sexually dimorphic (Fleagle et al, 1980; Frayer and Wolpoff, 1985; Simons et al, 2007; Harrison, 2013). Such widespread sexual size dimorphism does indicate an early origin. However, although the degree of dimorphism is difficult to determine in extinct species from the fossil record, there is no evidence of a marked increase in sexual size dimorphism in species considered to be early forms of catarrhines that evolved after the split from platyrrhines, over those that are thought to be earlier anthrapoids representing ancestors of both groups (Harrison, 2013). It is therefore difficult to suggest that the finding of early and rapid sexual selection occurring in catarrhine evolution aligns with evidence from the fossil record. However, it should be noted that the fossil record still only includes a very small percentage of all species that are thought to have ever existed, and the classification of extinct species into modern day clades is also difficult and ever changing, and so the very presence of sexual size dimorphism in such early anthropoids is one that supports an early origin for pronounced sexual size dimorphism in this group of primates.

The heightened sexual size dimorphism seen in catarrhines begs the question of why species within this clade have been subject to stronger sexual selection. The

finding of this study that this occurred early and rapidly in the evolution of catarrhines raises the question further to what it may have been that triggered the change in selection pressure at this time. With a clear association between mating system and sexual selection intensity with sexual size dimorphism (Kappeler, 1990; Plavcan and van Schaik, 1995; Plavcan, 2012; Cassini, 2020), as supported by the findings of a significant effect of mating system on sexual size dimorphism in this study, a shift in mating system in which more emphasis was placed on male-male competition may be a possible explanation for the intense sexual selection and the resulting rapid increase in sexual size dimorphism observed. Such an explanation requires looking back at what is known of the social dynamics of extinct groups of primates. Typically, social dynamics and mating systems of extinct species have been based on the sexual size dimorphism that is determined from fossil specimens (Plavcan, 2001). This of course is not ideal, as it presupposes sexual size dimorphism being a consequence of mating system. However, recent methods have changed this, and introduced ways of estimating ancestral social groupings and mating systems from known extant data (Kappeler and Pozzi, 2019).

Kappeler and Pozzi, 2019, in a study estimating ancestral social states of primates, determined the most likely social grouping at the root of catarrhines to be pair living, a state that the anthropoids had transitioned to earlier from an ancestral solitary state. They found that pair living most likely then transitioned to a multi-male/multi-female state as the cercopithecines evolved, which then further transitioned in several clades to the uni-male/multi-female groupings of many extant species (Kappeler and Pozzi, 2019). One explanation is that such a transition occurred as a response to increased predation risk from changes in circadian activity (Kappeler and Pozzi, 2019), and brought about increased competition between males for female mates, leading to intense sexual selection and increased sexual size dimorphism. However, Kappeler and Pozzi determined the most likely ancestral social state of Hominoidea to be pair living, suggesting that where the cercopithecines transitioned to a more complex state, the Hominoidea didn't. Clades within the hominids only later underwent transitions to the various social states of extant species. In contrast, the results of this study suggest intense sexual selection within catarrhines occurred prior to the divergence of the cercopithecines

54

and hominids, and so, if a transition in social state was the trigger for an increase in sexual selection, it would have had to occur at this time, and not, as Kappeler and Pozzi determined, only in cercopithecines after the divergence of these two groups.

Also, the same study of Kappeler and Pozzi determined that a similar transition from pair living to a multi-male/multi-female state took place at the root of platyrrhines (Kappeler and Pozzi, 2019). However, if this was the case, it didn't trigger the same increase in sexual dimorphism as I find in catarrhines. Whilst it may be possible for convergent adaptations to result in transitions to similar states in independent groups without the same increase in intrasexual competition, it is difficult to draw any firm conclusions.

It may also be possible that the relaxation of some constraint on male body size, allowing for runaway evolution of male size (Plavcan, 2001). Overall, whilst I find strong evidence for an increase in the intensity of selection for larger male size early on in catarrhine evolution, it is difficult to eliminate potential explanations with current knowledge of behaviours and ecology of species existing at that time, and it remains an intriguing question that continuing research will be required to answer. It should also be noted that whilst I find a significant effect of mating system on sexual size dimorphism, performing a primates-wide significance test as I have done may conflate the different patterns and association between mating system and sexual size dimorphism that previous authors have found, and fail to encapsulate the intricacies of the relationship within each clade (Plavcan and van Schaik, 1995; Plavcan, 2012).

4.5.   The origins of sexual size dimorphism in primates

The sexual size dimorphism observed in early catarrhine specimens are not the earliest examples of sexual size dimorphism in primates. There is evidence of dimorphism in Eocene adapid primates also (Gingerich, 1981, 1995; Krishtalka et al., 1991; Plavcan, 2001). Adapids are likely to represent a sister taxon to living strepsirrhines (Kay et al., 1997; Seiffert et al., 2009). If so, then sexual size dimorphism present in adapids means that the characteristic must have evolved on more than one occasion in primates, or alternatively, has extremely early origins

and extant strepsirrhines and tarsiers have since evolved to become monomorphic in size. Given that sexual size dimorphism has evolved convergently a number of times in different sets of animals, it would not be surprising if it has done so more than once in primates (Plavcan, 2001). Despite the dimorphism observed in adapids being used to support hypotheses that they are in fact a sister taxon to anthropoids, the variability of sexual size dimorphism in extant anthropoids suggests sexual size dimorphism in adapids alone makes for a relatively weak argument. Instead, the adapids more likely represent good evidence pointing towards convergent evolution of sexual size dimorphism among primates (Plavcan, 2001; Seiffert et al., 2009). The lack of sexual size dimorphism in fossil and sub-fossil strepsirrhines, including sub-fossil lemurs of far larger sizes than any of today's strepsirrhines, also suggests that where sexual size dimorphism evolved within the adapid lineage, it didn't in the strepsirrhines (Godfrey et al., 1993; Jungers et al., 2002).

Catarrhines are of course not the only extant primates that display sexual size dimorphism, with a number of platyrrhine species also doing so. This raises the question of whether sexual size dimorphism is a shared characteristic derived from a common ancestor in these groups, or if it has evolved independently in the two lineages. Evidence of sexual size dimorphism in two groups of extinct stem anthropoid, the parapithecids and oligopithecids of the late Eocene suggests that sexual size dimorphism is a shared trait between platyrrhines and catarrhines (Fleagle et al., 1980; Simons et al., 1999). I find evidence pointing towards sexual selection causing an increase in sexual size dimorphism early in catarrhine evolution, whereas I don't find such a pattern of selection early on in platyrrhine evolution that would indicate the evolution of sexual size dimorphism independently. However, not all platyrrhines display sexual size dimorphism, and so it could be possible that the characteristic has evolved independently only in certain lineages. I do find evidence that suggests sexual selection has likely led to increased sexual size dimorphism in the Capuchin monkeys (*Cebus & Sapajus*), but this is the only case, whereas it is not the only example of sexual size dimorphism in platyrrhines. Instead, I find in the callitrichids a pattern that is perhaps suggestive of an ancestral state of sexual size dimorphism, from which the callitrichids have evolved monomorphism by selection for reduced male size.

With no corresponding pattern of dwarfism in females, the simplest interpretation would be that sexual size dimorphism was present in the ancestors of callitrichids. My findings would suggest that an earlier origin of sexual size dimorphism in anthrapoids is more likely than convergent evolution. The intense sexual selection observed in catarrhines would then reflect the heightened sexual size dimorphism of this group.

However, I find no pattern of sexual selection – or any other form of selection – leading to sexual size dimorphism at any point earlier than the branch leading to catarrhines in primate evolution, despite sexual size dimorphism having to at some point evolved if it is a shared ancestral trait derived from early anthrapoids. It is perhaps possible that sexual size dimorphism, to a lesser degree, can be the result of a more passive explanation, in which male and female size comes to differ with time, as opposed to being the product of active selection. If this is the case, it would not be detectable by these methods which detect active selection and adaptive responses to changing circumstances. Exaggerated and extreme cases of sexual size dimorphism, as we see in the catarrhines are then likely driven by active and intense sexual selection.

Due to the scarcity of body mass data for extinct species, particularly independent data for males and females, fossil taxa were not included in this study. However, it is the case that extinct forms that fall outside the body mass range of extant species are known. The methods used in this study are the best yet at estimating ancestral states and being able to determine and explain long term evolutionary trends solely using data from extant species alone, it would be interesting in future works where it is possible to explore overall patterns when extinct clades are included, and to see what differences this may make to the observations of this study and others.

4.6.   Different patterns in different clades: what the rescaled trees show

4.6.1. Catarrhines

After the initial burst of accelerated rates in males I find early on in catarrhine evolution, there are a number of branches that have undergone accelerated rates. Many of these branches are suggested further instances of selection for larger male size, with the highest rate increases occurring in the most sexually dimorphic of species, such as *Mandrillus sphinx* and *Nasalis larvatus.* The baboons have also undergone sexual selection leading to increased sexual size dimorphism over the majority of catarrhines. These species are well known for having high instances of, and intense male-male competition, and so it is perhaps not surprising that I find strong sexual selection (Yeager, 1990; Plavcan and Van Schaik, 1997; Setchell and Dixon, 2001; Plavcan, 2012; Elton and Dunn, 2020). I find that *Mandrillus,* the genus containing both mandrills (*Mandrillus sphinx*) and drills (*Mandrillus leucophaeus*), have undergone selection for larger size in both sexes also, with accelerated rates on the branch leading to both species. The observation that body size has increased in both sexes suggests that natural selection has driven overall body size upwards. The greater rate evident in males compared to females also indicates a role for sexual selection. Mandrills (*Mandrillus sphinx*) live in hordes that can reach numbers as high as eight hundred individuals (Abernethy et al., 2002; White et al., 2010). This is the highest number for a cohesive group of primates known, and perhaps explains why such intense intrasexual competition is observed among males (Abernethy et al., 2002). As well as this, mandrills have a large home range (White et al., 2010). With drills (*Mandrillus leucophaeus)* also living in large groups (although far smaller than mandrills) and having relatively large home ranges, these ecological factors may be a potential reason for increased overall size in both sexes; larger groups and wider home ranges are associated with larger body size. Although, it is more likely that home range size increases in response to increased body size, as opposed to the other way round. (Milton and May, 1976; Clutton-Brock and Harvey, 1977). In the case of baboons, although they are among the largest anthropoids, this seems to be driven more by sexual selection than ecological factors, as I only find accelerated evolutionary rates in males.

I find selection for increased size in the branch leading to hominids in both sexes, suggesting that natural selection is behind the significantly larger size of hominids over that of the cercopithecidae. However, further sexual selection has also

occurred amongst the apes, most notably in the gorillas. Gorillas are the most dimorphic of the apes, and male gorillas are known to be highly aggressive towards one another, with the famed silverbacks controlling access to a harem of females (Breuer, 2008; Wright et al., 2021). Interestingly, despite showing sexual size dimorphism comparable with Gorillas, I find no indication of sexual selection in Orangutans. Orangutans, unlike Gorillas, live far more solitary lives, and although a resident male will still control the mating of groups of females, and compete with other males to do so, this competition occurs much less often (Te Boekhorst et al., 1990; Atmoko et al., 2009). Future research using similar methods on hominids specifically, with the inclusion of extinct species, would be interesting in shedding light on the evolution of social behavior within our own primate family.

One of the most unusual of catarrhines, in that they lack sexual size dimorphism, are the gibbons (*Hylobatids*). The lack of dimorphism in this group is less surprising perhaps when considering the monogamous mating system the gibbons have adopted, although this is in itself unusual among catarrhines (Brockelman, 2009). The findings of this study would suggest that the *Hylobatids* evolved to become monomorphic from an ancestral species that was sexually dimorphic. It is possible that this occurred as a result of a transition towards monogamy, with less emphasis on large size in males required to compete for females, optimum male size may have reduced. There is evidence in the fossil record of sexual dimorphism being present in extinct ape species. *Proconsul,* a genus whose position in history is still contended, but believed by some to be ancestral to all apes, having evolved after the split from the Cercopithecidae, is known to have been sexually dimorphic (Pickford, 1986; Cameron, 1991). There is also evidence of sexual size dimorphism in later extinct taxa of ape (Kelley and Qinghua, 1991; Kikuchi et al., 2018). However, I find no elevated rates of evolution on the branch leading to male gibbons that may be expected if males had undergone selection for smaller size, and so it is not possible to confirm that such selection has taken place.

The analyses indicate rather chaotic patterns among the macaques. Evolutionary rates within this clade are far more variable, in both sexes. Males and females have undergone accelerated rates in almost all species, with occurrences in both directions observed. It is likely that both sexual selection and natural selection have taken place given the range of body sizes and degrees of sexual size dimorphism

among extant macaques. It is possible that this rate heterogeneity is reflective of the ecological variation seen in the genus; macaques are highly adaptable and inhabit a range of habitats and climates, being able to tolerate and adapt to changing temperatures (Takasaki, 1981; Knight, 1999; Riley, 2008). Such ecological plasticity may explain the variation seen in evolutionary rates of macaque species, which are seemingly able to adapt quickly. It should also be considered that the genus *Macaca* is the largest of all catarrhines, and body mass data for some species is less reliable, having been taken from smaller sample numbers. It is therefore possible that low sample numbers have led to exaggeration of the variation of body masses seen in macaques, which in turn has led to higher variation in evolutionary rate also.

The same explanation may be behind the findings for the branch leading to *Semnopithecus hector:* females underwent a highly elevated rate of evolution in the direction of increased size, whereas the male rate remained unchanged. Further research into this species may be needed to help bolster knowledge of the behaviour and ecology, but the small sample number from which body mass data was taken make the results of this study somewhat unreliable in regard to *Semnopithecus hector.*

Finally, it is apparent that *Miopithecus talapoin,* the smallest of all catarrhines by some margin, has undergone dwarfism, with considerably elevated rates in both sexes in the direction of reduced size. This rate is slightly higher in males than in females, perhaps suggesting males have reduced in size to a higher degree than females. However, *Miopithecus* is still sexually dimorphic, counter to arguments for the association of body size and sexual size dimorphism refuted by the overall findings of this study.

4.6.2. Platyrrhines

The platyrrhines, whilst also mostly displaying sexual size dimorphism, but to a lesser extent than the catarrhines, follow a very different pattern. In fact, from the results of this study, it can be difficult to discern a pattern at all from the re-scaled branches of the evolutionary models run. In regard to sexual size dimorphism,

there are less obvious mechanisms at work. The most dimorphic of the platyrrhines are the *Alouatta,* which display sexual size dimorphism to a similar degree as that seen in many catarrhines. However, *Alouatta* belongs in the family Atelidae, in which the closely related genera *Ateles, Brachyteles* and *Lagothrix* typically display far less sexual size dimorphism. Interestingly, I do not find an elevated rate of evolution on the branch leading to the *Alouatta*, as might have been expected if sexual selection was the cause of this increased sexual size dimorphism over closely related species. I find elevated rates leading to the Atelidae in both sexes, suggesting natural selection has resulted in the large body size of extant species relative to other platyrrhines.

Alouatta display not only sexual size dimorphism, but males also have considerably larger hyoid bones, which allow them to make the loud calls for which they get their name, and some species exhibit sexual dichromatism. All of these traits are thought to have been sexually selected for (Van Belle and Bicca-Marques, 2014; Bergman et al., 2016). Sexual dichromatism, as well as the size differences in hyoid bones between males and females, suggest that sexual selection has played a part in the evolution of the genus, but I have not found evidence that it is the driving force behind the heightened sexual size dimorphism present. It is possible that whatever pressure is behind the strong selection that has driven body size upwards in Atelidae, has had more resistance from females, owing to the counter pressures of fecundity selection, and so relatively higher sexual size dimorphism has resulted. The increased sexual size dimorphism observed in *Alouatta* over other Atelidae does not seem to result from larger male size, but rather smaller female size; female *alouatta* are generally smaller than female *ateles, brachyteles* and *lagothrix*. With this in mind, could it be that sexual size dimorphism in alouatta is not the result of sexual size dimorphism, but instead fecundity selection in females? It is difficult to suggest either with any confidence based on the results of this study, with rate patterns not following what would be expected if either explanation were the case, and so it would seem apparent that the evolutionary patterns within this family are not clear cut, the variation in degree of sexual size dimorphism between *Alouatta* and their sister genus' is most likely multifactorial, and requires further study.

Elsewhere in the platyrrhines, there are instances of sexual selection having led to an increase in sexual size dimorphism. This is most notable in the capuchin monkeys (*Cebus* and *Sapajus),* in which we see an increased rate of evolution in males, but not in females, a pattern suggestive of sexual selection. The capuchin monkeys are more sexually dimorphic in size than the majority of other platyrrhines. Previous studies have reported that mating behaviour in the genus *Cebus* seems to be initiated be females more so than males, in contrast to the majority of polygynous primates (Phillips et al., 1994; Carosi et al., 2005). Female mating behaviour is most often directed towards the alpha male, which is often the largest male within a group, and so it is perhaps possible that female mate choice has had a larger role than male-male competition in driving male size upwards (Carosi et al., 2005). *Cebus* species have also been known to engage in infanticide, in which males kill the offspring of rival males (Bartlett et al., 1993; Ramirez-Llorens, 2008), a behaviour associated with sexual selection (Crockett and Sekulic, 1984; Palombit, 2015).

Within the Callitrichidae, a family that lacks sexual size dimorphism, we see some interesting patterns also. A number of branches have undergone accelerated rates of body size evolution in males, but not females. However, in contrast to other instances in which this has been the case that have indicated sexual selection for larger male size, here these accelerated rates represent selection for smaller body size in males. Thus, the Callitrichidae may be an interesting and unusual example of where sexual selection has acted to reduce sexual size dimorphism, with males being actively selected for smaller body size. This could be associated with the polyandrous mating system seen in this clade, in which male – male competition is all but nonexistent, although there is evidence of female-female competition as well as sperm competition (Araujo and Cordeiro de Sousa, 2008). Thus, another possibility is that natural selection has acted to decrease size in both sexes, but that females have also been subject to sexual selection for increased size owing to a polyandrous mating system. This would also explain the observed pattern of accelerated negative rates in males relative to females.

The small size of callitrichids is generally thought to have resulted from phyletic dwarfism (Ford, 1980; Preuss, 2019). However, I find a pattern compatible with dwarfism in only two species of Callitrichidae; *Callithrix humilis* and *Callithrix pygmaea,* the smallest species in the family. In these instances, I find elevated rates in the direction of reduced size in both males and females, indicative of phyletic dwarfism, however in no other species do I find elevated rates in females. This does not mean that dwarfism has not occurred, as average body size may well have decreased with time in this clade, however the reduction in size may not be the result of active selection for smaller size. If phyletic dwarfism has not been widespread among callitrichids as is generally regarded to be the case, then instead the explanation of a transition in mating system triggering sexual selection to act in a way that results in significant changes in sexual size dimorphism is an example of how mating system and sexual selection can interact to influence sexual size dimorphism (Marroig and Cheverud, 2005).

Overall, the platyrrhine tree appears difficult to interpret, and does not follow any obvious pattern throughout. Perhaps most notable is the number of branches on the male tree that have been compressed, with rate scalars less than one, which means they have undergone less, or slower evolution than would be expected under a Brownian motion model of evolution. There does not appear to be a pattern to these compressed branches, they are not concentrated in any particular area of the platyrrhine phylogeny and are instead widespread across it. The same pattern is not apparent in females. How these branches reflect sexual size dimorphism, or body size evolution in general is not very clear. It is likely that further and closer study into platyrrhine body size evolution is needed to better understand the significance of these instances.

4.6.3. Strepsirrhines

Strepsirrhines lack sexual size dimorphism, with males and females of all species approximating the same size, because of this it was expected that I would not see any indications of sexual selection, and that is the case. Male strepsirrhines have undergone fewer rate changes than male catarrhines or platyrrhines, whereas

females have undergone a higher number, all being accelerated rates suggesting faster than expected evolution.

Strepsirrhines are often considered a relatively ancestral group of primates, thought to be morphologically similar to the ancestral primate (Seiffert, 2007; Penna and Pozzi, 2019), largely due to their relatively small size as well as the presence of "ancestral" characteristics such as nocturnality (Goodman et al., 1993). However, the fossil record shows that strepsirrhines have undergone considerable morphological change throughout their history, alluding to the existence of species far larger than any extant species, including sub-fossil lemurs as large as Gorillas, and large lorisiforms (Godfrey et al., 2006; Godfrey and Jungers, 2010; Godfrey, 2016). Not only have strepsirrhines evolved such large sizes however, but it is also thought that nocturnal lemurs and the galagos have undergone body size reduction to reach the small sizes of today's species (Kappeler, 2012; Montgomery and Mundy, 2013; Penna and Pozzi, 2019). Such variable evolution in lemurs may represent a case of a line of least evolutionary resistance, in which changes in body size facilitate the exploitation of different ecologies (Marroig and Cheverud, 2005) Lemurs are also thought to represent a classic example of adaptive radiation, in which initial bursts of rapid evolution take place as species evolve to fill various niches, before diversification slows as niche saturation occurs (Simpson, 1953; Gillespie and Howarth, 2001; Herrera, 2017; Sakamoto, 2019). Although I may not have expected to find instances of sexual selection in strepsirrhines, I would be able to identify cases of phyletic dwarfism in which both sexes undergo accelerated evolutionary rates in the direction of reduced size.

I find substantial dwarfism within the Cheirogaleidae, as well as in *the* Lorisoidea, confirming the findings of previous studies (Montgomery and Mundy, 2013; Genin and Masters, 2016; Penna and Pozzi, 2019). However, the two dwarfism appears to follow a slightly different pattern in both clades, within the Cheirogaleidae, supporting previous findings (Martin, 1972; Herrera, 2017) I find a pattern compatible with adaptive radiation in regard to body size, in which clades have undergone rapid bursts of evolution towards smaller sizes and subsequently remained at small sizes, largely following rates similar to those expected under Brownian motion (Sakamoto, 2019). Extant lemurs represent only a small fraction

of the body range that has existed within the family, and it is likely that these results reflect this. Large bodied sub-fossil lemurs show that evolution has taken place in the opposing direction also, but also most likely followed a pattern of adaptive radiation (Godfrey, 2016). The Lorisoidea, in contrast, appear to show clade-wise shifts towards smaller sizes, whereby the majority of branches within the family have undergone elevated rates, suggestive of an increase in trait variation (Sakamoto et al., 2019).

These patterns suggest convergent cases of dwarfism have occurred in extant lineages of strepsirrhines and have results in a long-term evolutionary trend that is the opposite of Cope's rule, as seen in figure 4 a and b, in which strepsirrine body size has been decreasing with time. I also find that although rates are elevated in these instances in both sexes, the degree to which they are rescaled does differ between males and females. In the Cheirogaleidae I find a larger rate increase in males than in females, suggesting perhaps that males have undergone a larger body size decrease. In the Lorisoidea I find largely the opposite; many branches are rescaled more so in females than in males. Rate heterogeneity between the sexes perhaps means it is possible that given the sexual size dimorphism present in the adapid primates of the Eocene, that strepsirrhines have evolved from ancestors that did indeed display sexual size dimorphism. Nonetheless, given that there is a lack of sexual size dimorphism across all strepsirrhines, including in large bodies fossil taxa, this would seem an unlikely inference. All in all, the strepsirrhines perhaps represent the best example of all primates of the value that including fossil species can add to a data set, and studies using similar methods that do so where possible will add a great deal to the overall picture of strepsirrhine evolution.

4.6.4. Tarsiers

I find no cases of elevated or compressed evolutionary rates in either sex throughout the history of the tarsiers. Fossil tarsier specimens are known from as far back as the Eocene, and although they appear to have been far more widely distributed in the past, morphologically they have not changed a great deal

(Gingerich, 1984; Simons, 2003). Regarding sexual size dimorphism, tarsiers are monomorphic, and the lack of any instances of selection on body size in either sex perhaps tells us that social bahaviours and mating system have remained relatively constant throughout tarsier evolution also. The tarsiers appear to be a group that evolved to fill a niche a long time ago and have not had any great need to change or adapt in the time since.

5. Conclusions

The results of this study show that primate body mass evolution does not follow any one pattern, both body mass and sexual size dimorphism vary widely, and there are multiple routes leading to variation in both. However, there is strong evidence that sexual selection is the leading route through which sexual size

dimorphism has evolved in primates, particularly in catarrhines. Sexual selection and the resulting sexual size dimorphism are also most likely behind the observed trends of Cope's and Rensch's rule. Both trends result only from patterns that most likely reflect sexual selection. Sexual size dimorphism does not intrinsically increase with body size, and body size does not necessarily increase through evolutionary time. In the case of primates, sexual selection for larger male catarrhine size may have skewed the results of previous studies that have found primates to follow these rules. Consequently, based on the findings of this study, I would suggest that both Cope's and Rensch should be questioned as allometric "rules", and advance the argument that they are in fact statistical artefacts of sexual selection for increased male size.

This study demonstrates the exciting and interesting ways that modern phylogenetic comparative methods can be used to decouple evolutionary processes, such as sexual and natural selection, to answer long debated questions about the evolution of traits such as body size. Although studies based on data from extant species alone will always have limitations where they cannot fulfil the full range of traits that have ever existed within a group of animals, and the inclusion of fossil species in such methods will add a great deal more to the overall picture, whilst the fossil record remains difficult to include in such studies with reliable accuracy, the methods used here are among the best available to studying historical evolutionary processes and long term trends.

In regard to body size and sexual size dimorphism, the results of this study add intriguing answers to questions that are still widely debated. Similar future studies across a broader range of animal groups would be enlightening, and increase further our understanding of body mass evolution, determining whether the patterns I find in primates prove the norm across the animal kingdom, or an exception.

6. References

Abernethy, K.A., White, L.J. and Wickings, E.J., 2002. Hordes of mandrills (Mandrillus sphinx): extreme group size and seasonal male presence. *Journal of Zoology*, *258*(1), pp.131-137.

Abouheif, E. and Fairbairn, D.J., 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *The American Naturalist*, *149*(3), pp.540-562.

Alroy, J., 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science*, *280*(5364), pp.731-734.

Araújo, A. and de Sousa, M.B.C., 2008. Testicular volume and reproductive status of wild Callithrix jacchus. *International Journal of Primatology*, *29*, pp.1355-1364.

Atmoko, S.U., Setia, T.M., Goossens, B., James, S.S., Knott, C.D., Morrogh-Bernard, H.C., van Schaik, C.P. and van Noordwijk, M.A., 2009. Orangutan mating behavior and strategies. *Orangutans: Geographic variation in behavioral ecology and conservation*, pp.235-244.

Baker, J., Meade, A., Pagel, M. and Venditti, C., 2015. Adaptive evolution toward larger size in mammals. *Proceedings of the National Academy of Sciences*, *112*(16), pp.5093-5098.

Baker, J., Meade, A., Pagel, M. and Venditti, C., 2016. Positive phenotypic selection inferred from phylogenies. *Biological Journal of the Linnean Society*, *118*(1), pp.95-115.

Bartlett, T.Q., Sussman, R.W. and Cheverud, J.M., 1993. Infant killing in primates: a review of observed cases with specific reference to the sexual selection hypothesis. *American Anthropologist*, *95*(4), pp.958-990.

Barton, R.A. and Venditti, C., 2014. Rapid evolution of the cerebellum in humans and other great apes. *Current Biology*, *24*(20), pp.2440-2444.

Benson, R.B., Hunt, G., Carrano, M.T. and Campione, N., 2018. Cope's rule and the adaptive landscape of dinosaur body size evolution. *Palaeontology*, *61*(1), pp.13-48.

Bergman, T.J., Cortés-Ortiz, L., Dias, P.A., Ho, L., Adams, D., Canales-Espinosa, D. and Kitchen, D.M., 2016. Striking differences in the loud calls of howler monkey sister species (Alouatta pigra and A. palliata). *American Journal of Primatology*, *78*(7), pp.755-766.

Bidau, C.J. and Martinez, P.A., 2016. Sexual size dimorphism and Rensch's rule in Canidae. *Biological Journal of the Linnean Society*, *119*(4), pp.816-830.

Bokma, F., Godinot, M., Maridet, O., Ladevèze, S., Costeur, L., Solé, F., Gheerbrant, E., Peigné, S., Jacques, F. and Laurin, M., 2016. Testing for Depéret's rule (body size increase) in mammals using combined extinct and extant data. *Systematic biology*, *65*(1), pp.98-108.

Borghezan, E.D.A., Pinto, K.D.S., Zuanon, J. and Pires, T.H.D.S., 2019. Someone like me: Size-assortative pairing and mating in an Amazonian fish, sailfin tetra Crenuchus spilurus. *PloS one*, *14*(9), p.e0222880.

Bradley, B.J. and Mundy, N.I., 2008. The primate palette: the evolution of primate coloration. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *17*(2), pp.97-111.

Breuer, T., 2008. Male reproductive success in wild western gorillas (Gorilla gorilla). *University of Leipzig, Leipzig*.

Brockelman, W.Y., 2009. Ecology and the social system of gibbons. *The gibbons: New perspectives on small ape socioecology and population biology*, pp.211-239.

Butler, R.J. and Goswami, A., 2008. Body size evolution in Mesozoic birds: little evidence for Cope's rule. *Journal of Evolutionary Biology*, *21*(6), pp.1673-1682.

Cameron, D.W., 1991. Sexual dimorphism in the early Miocene species of Proconsul from the Kisingiri Formation of East Africa: a morphometric examination using multivariate statistics. *Primates*, *32*, pp.329-343.

Cardini, A. and Elton, S., 2008. Variation in guenon skulls (I): species divergence, ecological and genetic differences. *Journal of Human Evolution*, *54*(5), pp.615-637.

Caro, T., 2021. When animal coloration is a poor match. *Evolutionary Ecology*, *35*(1), pp.1-13.

Carosi, M., Linn, G.S. and Visalberghi, E., 2005. The sexual behavior and breeding system of tufted capuchin monkeys (Cebus apella). *Advances in the Study of Behavior*, *35*, pp.105-149.

Cassini, M.H., 2017. Role of fecundity selection on the evolution of sexual size dimorphism in mammals. *Anim Behav*, *128*, pp.1-4.

Cassini, M.H., 2020. Sexual size dimorphism and sexual selection in primates. *Mammal review*, *50*(3), pp.231-239.

Charnov, E.L. and Berrigan, D., 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology: Issues, News, and Reviews*, *1*(6), pp.191-194.

Clauset, A. and Erwin, D.H., 2008. The evolution and distribution of species body size. *Science*, *321*(5887), pp.399-401.

Clutton-Brock, T.H., Harvey, P.H. and Rudder, B., 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*, *269*, pp.797-800.

Clutton-Brock, T.H., Hodge, S.J., Spong, G., Russell, A.F., Jordan, N.R., Bennett, N.C., Sharpe, L.L. and Manser, M.B., 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature*, *444*(7122), pp.1065-1068.

Cooney, C.R., Varley, Z.K., Nouri, L.O., Moody, C.J., Jardine, M.D. and Thomas, G.H., 2019. Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature communications*, *10*(1), p.1773.

Cooper, N. and Purvis, A., 2010. Body size evolution in mammals: complexity in tempo and mode. *The American Naturalist*, *175*(6), pp.727-738.

Cooper, V.J. and Hosey, G.R., 2003. Sexual dichromatism and female preference in Eulemur fulvus subspecies. *International Journal of Primatology*, *24*, pp.1177-1188.

Cooper, M., 2018. Centrobolus size dimorphism breaks Rensch's rule. *Arthropods*, *7*(3), p.48.

Crockett, C.M., 2003. Re-evaluating the sexual selection hypothesis for infanticide by Alouatta males. *Sexual selection and reproductive competition in primates: New perspectives and directions*, pp.327-365.

Darwin, C., 1831. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life (*Vol. 11859). London: John Murray.

Delson, E., Terranova, C.J., Jungers, W.L., Sargis, E.J. and Jablonski, N.G., 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. Anthropological papers of the AMNH; no. 83.

DeVore, I. and Washburn, S.L., 2017. Baboon ecology and human evolution. In *African ecology and human evolution* (pp. 335-367). Routledge.

Dunbar, R.I., 1995. Neocortex size and group size in primates: a test of the hypothesis. *Journal of human evolution*, *28*(3), pp.287-296.

A.E., Maitner, B.S., Razafindratsima, O.H., Simmons, M.C. and Roy, C.L., 2013. Body size and sexual size dimorphism in primates: influence of climate and net primary productivity. *Journal of Evolutionary Biology*, *26*(11), pp.2312-2320.

Elton, S. and Dunn, J., 2020. Baboon biogeography, divergence, and evolution: Morphological and paleoecological perspectives. *Journal of Human Evolution*, *145*, p.102799.

Fairbairn, D.J., 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual review of ecology and systematics*, *28*(1), pp.659-687.

Felsenstein, J., 1985. Phylogenies and the comparative method. *The American Naturalist*, *125*(1), pp.1-15.

Fisher, R. A., 1930. *The genetical theory of natural selection.* Clarendon Press.

Fisher, J.T., Anholt, B. and Volpe, J.P., 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and evolution*, *1*(4), pp.517-528.

Fleagle, J.G., Kay, R.F. and Simons, E.L., 1980. Sexual dimorphism in early anthropoids. *Nature*, *287*(5780), pp.328-330.

Ford, S.M., 1980. Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in Platyrrhini. *Primates*, *21*, pp.31-43.

Foster, J.B., 1964. Evolution of mammals on islands. *Nature*, *202*(4929), pp.234-235.

Frayer, D.W. and Wolpoff, M.H., 1985. Sexual dimorphism. *Annual Review of Anthropology*, *14*(1), pp.429-473.

Gadgil, M., 1972. Male dimorphism as a consequence of sexual selection. *The American Naturalist*, *106*(951), pp.574-580.

Galán-Acedo, C., Arroyo-Rodríguez, V., Cudney-Valenzuela, S.J. and Fahrig, L., 2019. A global assessment of primate responses to landscape structure. *Biological Reviews*, *94*(5), pp.1605-1618.

Génin, F., Masters, J.C., Lehman, S.M., Radespiel, U. and Zimmermann, E., 2016. The physiology of phyletic dwarfism in Cheirogaleidae. *The dwarf and mouse lemurs of Madagascar*, pp.317-334.

Gillespie, R.G., Howarth, F.G. and Roderick, G.K., 2001. Adaptive radiation. *Encyclopedia of biodiversity*, *1*, pp.25-44.

Gingerich, P.D., 1981. Variation, sexual dimorphism, and social structure in the early Eocene horse Hyracotherium (Mammalia, Perissodactyla). *Paleobiology*, *7*(4), pp.443-455.

Gingerich, P.D., 1984. Paleobiology of tarsiiform primates. *Biology of tarsiers (ed. C. Niemitz)*, pp.33-44.

Gingerich, P.D., 1985. Species in the fossil record: concepts, trends, and transitions. *Paleobiology*, *11*(1), pp.27-41.

Godfrey, L.R., Lyon, S.K. and Sutherland, M.R., 1993. Sexual dimorphism in large-bodied primates: the case of the subfossil lemurs. *American Journal of Physical Anthropology*, *90*(3), pp.315-334.

Godfrey, L.R., Schwartz, G.T., Samonds, K.E., Jungers, W.L. and Catlett, K.K., 2006. The secrets of lemur teeth. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *15*(4), pp.142-154.

Godfrey, L.R., Jungers, W.L. and Burney, D.A., 2010. Subfossil lemurs of Madagascar. *Cenozoic mammals of Africa*, pp.351-367.

Godfrey, L.R., 2016. Subfossil lemurs. *The international encyclopedia of primatology*, pp.1-5.

Goldbogen, J.A., 2018. Physiological constraints on marine mammal body size. *Proceedings of the National Academy of Sciences*, *115*(16), pp.3995-3997.

Goodman, S.M., O'Connor, S. and Langrand, O., 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. *Lemur social systems and their ecological basis*, pp.51-66.

Gordon, A.D., 2006. Scaling of size and dimorphism in primates II: macroevolution. *International Journal of Primatology*, *27*, pp.63-105.

Gould, S.J., 1997. Cope's rule as psychological artefact. *Nature*, *385*(6613), pp.199-200.

Greenfield, L.O., 1996. Correlated response of homologous characteristics in the anthropoid anterior dentition. *Journal of human evolution*, *31*(1), pp.1-19.

Haldane, J.B.S., 1937. The effect of variation of fitness. *The American Naturalist*, *71*(735), pp.337-349.

Harrison, T., 2013. Catarrhine origins. *A companion to paleoanthropology*, pp.376-396.

Harmon, L.J., Losos, J.B., Jonathan Davies, T., Gillespie, R.G., Gittleman, J.L., Bryan Jennings, W., Kozak, K.H., McPeek, M.A., Moreno-Roark, F., Near, T.J. and Purvis, A., 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, *64*(8), pp.2385-2396.

Harvey PH, Kavanagh M, Clutton-Brock TH. 1978. Sexual dimor-phism in primate teeth. J Zool Lond 186:474–485.

Harvey, P. H. and Pagel, M. D. 1991. *The comparative method in evolutionary biology*. – Oxford Univ. Press.

Herrera, J.P., 2017. Testing the adaptive radiation hypothesis for the lemurs of Madagascar. *Royal Society open science*, *4*(1), p.161014.

Hone, D.W. and Benton, M.J., 2005. The evolution of large size: how does Cope's Rule work?. *Trends in ecology & evolution*, *20*(1), pp.4-6.

Jablonski, D., 1997. Body-size evolution in Cretaceous molluscs and the status of Cope's rule. *Nature*, *385*(6613), pp.250-252.

Jablonski, N.G., Whitfort, M.J., Roberts-Smith, N. and Qinqi, X., 2000. The influence of life history and diet on the distribution of catarrhine primates during the Pleistocene in eastern Asia. *Journal of Human Evolution*, *39*(2), pp.131-157.

Jones, K.E. and Purvis, A., 1997. An optimum body size for mammals? Comparative evidence from bats. *Functional Ecology*, *11*(6), pp.751-756.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C. and Connolly, C., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and

recently extinct mammals: Ecological Archives E090-184. *Ecology*, *90*(9), pp.2648-2648.

Jungers, W.L., Godfrey, L.R., Simons, E.L., Wunderlich, R.E., Richmond, B.G. and Chatrath, P.S., 2002. Ecomorphology and behavior of giant extinct lemurs from Madagascar. *Reconstructing behavior in the primate fossil record*, pp.371-411.

Kay, R.F., Ross, C. and Williams, B.A., 1997. Anthropoid origins. *Science*, *275*(5301), pp.797-804.

Kappeler, P.M., 1990. The evolution of sexual size dimorphism in prosimian primates. *American Journal of Primatology*, *21*(3), pp.201-214.

Kappeler, P.M. and van Schaik, C.P., 2002. Evolution of primate social systems. *International journal of primatology*, *23*, pp.707-740.

Kappeler, P.M., 2012. The behavioral ecology of strepsirrhines and tarsiers. *The evolution of primate societies*, *17*, p.42.

Kappeler, P.M. and Pozzi, L., 2019. Evolutionary transitions toward pair living in nonhuman primates as stepping stones toward more complex societies. *Science advances*, *5*(12), p.eaay1276.

Kelley, J. and Qinghua, X., 1991. Extreme sexual dimorphism in a Miocene hominoid. *Nature*, *352*(6331), pp.151-153.

Kemp, T.S., 2005. *The origin and evolution of mammals*. Oxford University Press on Demand.

Kikuchi, Y., Nakatsukasa, M., Tsujikawa, H., Nakano, Y., Kunimatsu, Y., Ogihara, N., Shimizu, D., Takano, T., Nakaya, H., Sawada, Y. and Ishida, H., 2018. Sexual dimorphism of body size in an African fossil ape, Nacholapithecus kerioi. *Journal of human evolution*, *123*, pp.129-140.

Kingsolver, J.G. and Pfennig, D.W., 2004. Individual-level selection as a cause of Cope's rule of phyletic size increase. *Evolution*, *58*(7), pp.1608-1612.

Knight, J., 1999. Monkeys on the move: the natural symbolism of people-macaque conflict in Japan. *The Journal of Asian Studies*, *58*(3), pp.622-647.

Kodric-Brown, A., 1985. Female preference and sexual selection for male coloration in the guppy (Poecilia reticulata). *Behavioral Ecology and Sociobiology*, *17*, pp.199-205.

Krause, D.W., 2003. Late Cretaceous vertebrates of Madagascar: a window into Gondwanan biogeography at the end of the age of dinosaurs. *The natural history of Madagascar*.

Krishtalka, L., Stucky, R.K. and Beard, K.C., 1990. The earliest fossil evidence for sexual dimorphism in primates. *Proceedings of the National Academy of Sciences*, *87*(13), pp.5223-5226.

Lande, R., 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, pp.292-305.

Lande, R., 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. *Sexual selection: testing the alternatives*, pp.83-94.

Leutenegger, W. and Cheverud, J., 1982. Correlates of sexual dimorphism in primates: ecological and size variables. *International Journal of Primatology*, *3*, pp.387-402.

Leutenegger, W. and Kelly, J.T., 1977. Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates*, *18*, pp.117-136.

Cheverud, J.M., Dow, M.M. and Leutenegger, W., 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution*, *39*(6), pp.1335-1351.

Lindenfors, P. and Tullberg, B.S., 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. *Biological Journal of the Linnean Society*, *64*(4), pp.413-447.

Lindenfors, P. and Tullberg, B.S., 2006. Lowering sample size in comparative analyses can indicate a correlation where there is none: example from Rensch's rule in primates. *Journal of Evolutionary Biology*, *19*(4), pp.1346-1351.

Lindenfors, P., Gittleman, J.L. and Jones, K.E., 2007. Sexual size dimorphism in mammals. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*, *16*, p.26.

Marroig, G. and Cheverud, J.M., 2005. Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World monkeys. *Evolution*, *59*(5), pp.1128-1142.

Martin RD. 1984. Scaling effects and adaptive strate-gies in mammalian lactation. Symp Zool Soc Lond51:87-117.

Martin, Robert D., Lesley A. Willner, and Andrea Dettling. 1994. The evolution of sexual size dimorphism in primates. In *The differences between the sexes*. Roger V. Short and Evan Balaban, eds. Pp. 159–200. Cambridge: Cambridge University Press.

Martinez, P., 2018. The comparative method in biology and the essentialist trap. *Frontiers in ecology and evolution*, *6*, p.130.

Maurer, B.A., Brown, J.H., Rusler, R.D. 1992 The micro and macro in body size evolution. *Evolution*, 46, 939953.

McKinney, M.L., 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual review of ecology and systematics*, *28*(1), pp.495-516.

McLain, D.K., 1993. Cope's rules, sexual selection, and the loss of ecological plasticity. *Oikos*, pp.490-500.

McLean, C.J., Garwood, R.J. and Brassey, C.A., 2018. Sexual dimorphism in the Arachnid orders. *PeerJ*, *6*, p.e5751.

Pagel, M. and Meade, A., 2017. Bayes traits V3. *Comput. Progr. Doc.*

Milton, K. and May, M.L., 1976. Body weight, diet and home range area in primates. *Nature*, *259*(5543), pp.459-462.

Monroe, M.J. and Bokma, F., 2010. Little evidence for Cope's rule from Bayesian phylogenetic analysis of extant mammals. *Journal of evolutionary biology*, *23*(9), pp.2017-2021.

Montgomery, S.H., Capellini, I., Barton, R.A. and Mundy, N.I., 2010. Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and Homo floresiensis. *BMC biology*, *8*(1), pp.1-19.

Montgomery, S.H. and Mundy, N.I., 2013. Parallel episodes of phyletic dwarfism in callitrichid and cheirogaleid primates. *Journal of evolutionary biology*, *26*(4), pp.810-819.

Nelson, G.J., 1970. Outline of a theory of comparative biology. *Systematic Zoology*, *19*(4), pp.373-384.

Niemitz, C. ed., 1984. *Biology of tarsiers* (pp. 191-226). New York: G. Fischer.

Nunn, C.L., 2011. *The comparative approach in evolutionary anthropology and biology*. University of Chicago Press.

O'Mara, M.T., Gordon, A.D., Catlett, K.K., Terranova, C.J. and Schwartz, G.T., 2012. Growth and the development of sexual size dimorphism in lorises and galagos. *American journal of physical anthropology*, *147*(1), pp.11-20.

O'Meara, B.C., 2012. Evolutionary inferences from phylogenies: a review of methods. *Annual Review of Ecology, Evolution, and Systematics*, *43*, pp.267-285.

Opie, C., Atkinson, Q.D. and Shultz, S., 2012. The evolutionary history of primate mating systems. *Communicative & Integrative Biology*, *5*(5), pp.458-461.

Pagel, M., Meade, A. and Barker, D., 2004. Bayesian estimation of ancestral character states on phylogenies. *Systematic biology*, *53*(5), pp.673-684.

Palombit, R.A., 2015. Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology*, *7*(6), p.a017640.

Penna, A. and Pozzi, L., 2019, March. The evolution of body size in Strepsirrhine primates. In *AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY* (Vol. 168, pp. 188-188). 111 RIVER ST, HOBOKEN 07030-5774, NJ USA: WILEY.

Phillips, K.A., Bernstein, I.S., Dettmer, E.L., Devermann, H. and Powers, M., 1994. Sexual behavior in brown capuchins (Cebus apella). *International Journal of Primatology*, *15*, pp.907-917.

Pickford, M., 1986. Sexual dimorphism in Proconsul. *Human evolution*,*1*, pp.111-148.

Plavcan, J.M., 2001. Sexual dimorphism in primate evolution. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *116*(S33), pp.25-53.

Plummer, M., Best, N., Cowles, K. and Vines, K., 2006. CODA: convergence diagnosis and output analysis for MCMC. *R news*, *6*(1), pp.7-11.

Procter, D.S., Moore, A.J. and Miller, C.W., 2012. The form of sexual selection arising from male–male competition depends on the presence of females in the social environment. *Journal of Evolutionary Biology*, *25*(5), pp.803-812.

Peters, R.H. and Peters, R.H., 1986. *The ecological implications of body size* (Vol. 2). Cambridge university press.

Plavcan, J.M. and Van Schaik, C.P., 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *103*(1), pp.37-68.

Plavcan, J.M., 2012. Sexual size dimorphism, canine dimorphism, and male-male competition in primates: where do humans fit in?. *Human Nature*, *23*, pp.45-67.

Pozzi, L., Disotell, T.R. and Masters, J.C., 2014. A multilocus phylogeny reveals deep lineages within African galagids (Primates: Galagidae). *BMC evolutionary biology*, *14*(1), pp.1-18.

Preuss, T.M., 2019. Critique of pure marmoset. *Brain, behavior and evolution*, *93*(2-3), pp.92-107.

Rakotonirina, H., Kappeler, P.M. and Fichtel, C., 2017. Evolution of facial color pattern complexity in lemurs. *Scientific Reports*, *7*(1), p.15181.

Ramírez-Llorens, P., Di Bitetti, M.S., Baldovino, M.C. and Janson, C.H., 2008. Infanticide in black capuchin monkeys (Cebus apella nigritus) in Iguazú National Park, Argentina. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *70*(5), pp.473-484.

Rensch, B., 1948. Histological changes correlated with evolutionary changes of body size. *Evolution*, pp.218-230.

Rensch, B., 1959. Evolution above the species level. In *Evolution Above the Species Level*. Columbia University Press.

Revell, L.J., Harmon, L.J. and Collar, D.C., 2008. Phylogenetic signal, evolutionary process, and rate. *Systematic biology*, *57*(4), pp.591-601.

Riley, E.P., 2008. Ranging patterns and habitat use of Sulawesi Tonkean macaques (Macaca tonkeana) in a human-modified habitat. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *70*(7), pp.670-679.

Rose, K.D., 1994. The earliest primates. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(5), pp.159-173.

Rowe, N. and Myers, M. eds., 2016. *All the world's primates* (Vol. 777, pp. 45-46). Charlestown: Pogonias Press.

Russell, E.S., 1916. *Form and function: A contribution to the history of animal morphology*. University of Glasgow (United Kingdom).

Rylands, A.B. and Mittermeier, R.A., 2009. The diversity of the New World primates (Platyrrhini): an annotated taxonomy. *South American primates: comparative perspectives in the study of behavior, ecology, and conservation*, pp.23-54.

Sahney, S., Benton, M.J. and Ferry, P.A., 2010. Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. *Biology letters*, *6*(4), pp.544-547.

Sakamoto, M., Ruta, M. and Venditti, C., 2019. Extreme and rapid bursts of functional adaptations shape bite force in amniotes. *Proceedings of the Royal Society B*, *286*(1894), p.20181932.

Schrago, C.G. and Russo, C.A., 2003. Timing the origin of New World monkeys. *Molecular biology and evolution*, *20*(10), pp.1620-1625.

Seiffert, E.R., 2007. Early evolution and biogeography of lorisiform strepsirrhines. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *69*(1), pp.27-35.

Seiffert, E.R., Perry, J.M., Simons, E.L. and Boyer, D.M., 2009. Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. *Nature*, *461*(7267), pp.1118-1121.

Setchell, J.M. and Dixson, A.F., 2001. Changes in the secondary sexual adornments of male mandrills (Mandrillus sphinx) are associated with gain and loss of alpha status. *Hormones and Behavior*, *39*(3), pp.177-184.

Silcox, M.T., Bloch, J.I., Boyer, D.M., Chester, S.G. and López-Torres, S., 2017. The evolutionary radiation of plesiadapiforms. *Evolutionary Anthropology: Issues, News, and Reviews*, *26*(2), pp.74-94.

Slicox, M.T., 2014. Primate Origins and the Plesiadapiforms. *Nature Education Knowledge*, *5*(3), p.1.

Silcox, M.T., Sargis, E.J., Bloch, J.I. and Boyer, D.M., 2007. Primate origins and supraordinal relationships: morphological evidence. *Handbook of paleoanthropology*, *2*, pp.831-859.

Simons, E.L., Plavcan, J.M. and Fleagle, J.G., 1999. Canine sexual dimorphism in Egyptian Eocene anthropoid primates: Catopithecus and Proteopithecus. *Proceedings of the National Academy of Sciences*, *96*(5), pp.2559-2562.

Simons, E.L., 2003. The fossil record of tarsier evolution. *Tarsiers: Past, Present, and Future. Rutgers University Press, New Brunswick*, pp.9-34.

Simons, E.L., Seiffert, E.R., Ryan, T.M. and Attia, Y., 2007. A remarkable female cranium of the early Oligocene anthropoid Aegyptopithecus zeuxis (Catarrhini, Propliopithecidae). *Proceedings of the National Academy of Sciences*, *104*(21), pp.8731-8736.

Simpson, G.G., 1953. The major features of evolution. In *The major features of evolution*. Columbia University Press.

Smith, R.J. and Cheverud, J.M., 2002. Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's rule in primates. *International Journal of Primatology*, *23*, pp.1095-1135.

Smith, R.J. and Jungers, W.L., 1997. Body mass in comparative primatology. *Journal of Human evolution*, *32*(6), pp.523-559.

Soligo C. 2001. Adaptations and ecology of the earliest primates. Ph.D. dissertation, University of Zürich.

Soligo, C., 2006. Correlates of body mass evolution in primates. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *130*(3), pp.283-293.

Soligo, C. and Smaers, J.B., 2016. Contextualising primate origins–an ecomorphological framework. *Journal of Anatomy*, *228*(4), pp.608-629.

 Stanley, S.M., 1973. An explanation for Cope's rule. *Evolution*, pp.1-26.

Sussman, R.W., Tab Rasmussen, D. and Raven, P.H., 2013. Rethinking primate origins again. *American Journal of Primatology*, *75*(2), pp.95-106.

Székely, T., Freckleton, R.P. and Reynolds, J.D., 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences*, *101*(33), pp.12224-12227.

Takasaki, H., 1981. Troop size, habitat quality, and home range area in Japanese macaques. *Behavioral Ecology and Sociobiology*, *9*, pp.277-281.

Tattersall, I., 2006. The concept of cathemerality: history and definition. *Folia primatologica*, *77*(1-2), pp.7-14.

Tavaré, S., Marshall, C.R., Will, O., Soligo, C. and Martin, R.D., 2002. Using the fossil record to estimate the age of the last common ancestor of extant primates. *Nature*, *416*(6882), pp.726-729.

Te Boekhorst, I.J., Schürmann, C.L. and Sugardjito, J., 1990. Residential status and seasonal movements of wild orang-utans in the Gunung Leuser Reserve (Sumatera, Indonesia). *Animal Behaviour*, *39*(6), pp.1098-1109.

Tobias, J.A., Montgomerie, R. and Lyon, B.E., 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1600), pp.2274-2293.

Van Belle, S. and Bicca-Marques, J.C., 2015. Insights into reproductive strategies and sexual selection in howler monkeys. *Howler monkeys: Behavior, ecology, and conservation*, pp.57-84.

Venditti, C., Meade, A. and Pagel, M., 2011. Multiple routes to mammalian diversity. *Nature*, *479*(7373), pp.393-396.

Wang, W., 2009. New discoveries of Gigantopithecus blacki teeth from Chuifeng Cave in the Bubing Basin, Guangxi, south China. *Journal of Human Evolution*, *57*(3), pp.229-240.

Webb, T.J. and Freckleton, R.P., 2007. Only half right: species with female-biased sexual size dimorphism consistently break Rensch's rule. *PLoS One*, *2*(9), p.e897.

Weckerly, F.W., 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy*, *79*(1), pp.33-52.

White, E.C., Dikangadissi, J.T., Dimoto, E., Karesh, W.B., Kock, M.D., Ona Abiaga, N., Starkey, R., Ukizintambara, T., White, L.J. and Abernethy, K.A., 2010. Home-range use by a large horde of wild Mandrillus sphinx. *International Journal of Primatology*, *31*, pp.627-645.

Wright, E., Grawunder, S., Ndayishimiye, E., Galbany, J., McFarlin, S.C., Stoinski, T.S. and Robbins, M.M., 2021. Chest beats as an honest signal of body size in male mountain gorillas (Gorilla beringei beringei). *Scientific Reports*, *11*(1), p.6879.

Yeager, C.P., 1990. Proboscis monkey (Nasalis larvatus) social organization: group structure. *American Journal of Primatology*, *20*(2), pp.95-106.

Yoder, A.D. and Yang, Z., 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Molecular Ecology*, 1*3*(4), pp.757-773.

7. Appendix

Species and data used in this study

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Allenopithecus_nigroviridis	6.130	3.180	1.93	Smith and Jungers, 1997	Polygynandrous	Both
Allocebus_trichotis	0.083	0.078	1.06	Rowe and Myers, 2017	Monogamous	Arboreal
Alouatta_belzebul	7.270	5.520	1.32	Smith and Jungers, 1997	Polygynous	Arboreal
Alouatta_caraya	6.420	4.330	1.48	Smith and Jungers, 1997	Polygynandrous	Arboreal
Alouatta_guariba	6.730	4.350	1.55	Rowe and Myers, 2017	Polygynous	Arboreal
Alouatta_palliata	7.150	5.350	1.34	Smith and Jungers, 1997	Polygynous	Arboreal
Alouatta_pigra	7.500	5.610	1.34	Rowe and Myers, 2017	Polygynous	Arboreal
Alouatta_seniculus	6.690	5.210	1.28	Smith and Jungers, 1997	Polygynous	Arboreal
Aotus_azarai	1.180	1.230	0.96	Smith and Jungers, 1997	Monogamous	Arboreal
Aotus_griseimembra	1.009	0.923	1.09	Rowe and Myers, 2017	Monogamous	Arboreal
Aotus_lemurinus	0.918	0.874	1.05	Smith and Jungers, 1997	Monogamous	Arboreal
Aotus_nancymaae	0.794	0.780	1.02	Smith and Jungers, 1997	Monogamous	Arboreal
Aotus_nigriceps	0.875	1.040	0.84	Smith and Jungers, 1997	Monogamous	Arboreal
Aotus_trivirgatus	0.813	0.736	1.10	Smith and Jungers, 1997	Monogamous	Arboreal
Aotus_vociferans	0.708	0.698	1.01	Smith and Jungers, 1997	Monogamous	Arboreal
Arctocebus_calabarensis	0.310	0.310	1.00	Rowe and Myers, 2017	Polygynous	Arboreal
Ateles_belzebuth	8.290	7.850	1.06	Smith and Jungers, 1997	Polygynandrous	Arboreal
Ateles_fusciceps	9.100	9.163	0.99	Smith and Jungers, 1997	Polygynandrous	Arboreal
Ateles_geoffroyi	7.780	7.290	1.07	Smith and Jungers, 1997	Polygynandrous	Arboreal
Ateles_paniscus	9.110	8.440	1.08	Smith and Jungers, 1997	Polygynandrous	Arboreal
Avahi_cleesei	1.000	1.000	1.00	Rowe and Myers, 2017	Monogamous	Arboreal
Avahi_laniger	1.030	1.320	0.78	Smith and Jungers, 1997	Monogamous	Arboreal
Avahi_occidentalis	0.810	0.780	1.04	Smith and Jungers, 1997	Monogamous	Arboreal
Brachyteles_arachnoides	9.610	8.070	1.19	Smith and Jungers, 1997	Polygynandrous	Arboreal
Brachyteles_hypoxanthus	9.600	8.400	1.14	Rowe and Myers, 2017	Polygynandrous	Arboreal
Cacajao_ayresi	4.500	3.100	1.45	Rowe and Myers, 2017	Monogamous	Arboreal
Cacajao_calvus	3.450	2.880	1.20	Smith and Jungers, 1997	Monogamous	Arboreal
Cacajao_hosomi	4.500	3.100	1.45	Rowe and Myers, 2017	-	Arboreal
Cacajao_melanocephalus	3.160	2.710	1.17	Smith and Jungers, 1997	-	Arboreal
Callicebus_nigrifrons	1.350	1.300	1.04	Rowe and Myers, 2017	Monogamous	Arboreal
Callicebus_personatus	1.270	1.380	0.92	Smith and Jungers, 1997	Monogamous	Arboreal
Callimico_goeldii	0.499	0.468	1.07	Rowe and Myers, 2017	Polyandrous	Arboreal
Callithrix_argentata	0.330	0.360	0.92	Smith and Jungers, 1997	Polyandrous	Arboreal
Callithrix_aurita	0.453	0.431	1.05	Rowe and Myers, 2017	Monogamous	Arboreal

81

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Callithrix_emiliae	0.313	0.330	0.95	Smith and Jungers, 1997	-	Arboreal
Callithrix_geoffroyi	0.324	0.369	0.88	Rowe and Myers, 2017	Polyandrous	Arboreal
Callithrix_humeralifera	0.360	0.380	0.95	Rowe and Myers, 2017	-	Arboreal
Callithrix_humilis	0.136	0.168	0.81	Rowe and Myers, 2017	Polyandrous	Arboreal
Callithrix_jacchus	0.362	0.381	0.95	Rowe and Myers, 2017	Polyandrous	Arboreal
Callithrix_mauesi	0.345	0.398	0.87	Smith and Jungers, 1997	-	Arboreal
Callithrix_melanura	0.406	0.380	1.07	Rowe and Myers, 2017	Polyandrous	-
Callithrix_penicillata	0.344	0.307	1.12	Smith and Jungers, 1997	Monogamous	Arboreal
Callithrix_pygmaea	0.110	0.112	0.98	Smith and Jungers, 1997	Polyandrous	Arboreal
Callithrix_saterei	0.470	0.412	1.14	Rowe and Myers, 2017	-	Arboreal
Carlito_syrichta	0.135	0.119	1.13	Rowe and Myers, 2017	Polygynous	Arboreal
Cebus_albifrons	3.180	2.290	1.39	Smith and Jungers, 1997	Polygynandrous	Both
Cebus_capucinus	3.680	2.540	1.45	Smith and Jungers, 1997	Polygynandrous	Arboreal
Cebus_kaapori	3.050	2.150	1.42	Rowe and Myers, 2017	Polygynandrous	Arboreal
Cebus_olivaceus	3.000	2.500	1.20	Rowe and Myers, 2017	Polygynous	Arboreal
Cercocebus_agilis	9.500	5.660	1.68	Smith and Jungers, 1997	-	Both
Cercocebus_atys	11.000	6.200	1.77	Smith and Jungers, 1997	Polygynandrous	Terrestrial
Cercocebus_galeritus	9.610	5.260	1.83	Smith and Jungers, 1997	Polygynous	Both
Cercocebus_torquatus	9.470	5.500	1.72	Smith and Jungers, 1997	Polygynandrous	Both
Cercopithecus_ascanius	3.700	2.920	1.27	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_campbelli	4.500	2.700	1.67	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_cephus	4.290	2.880	1.49	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_diana	5.200	3.900	1.33	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_erythrogaster	4.100	2.400	1.71	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_erythrotis	3.600	2.900	1.24	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_hamlyni	5.490	3.360	1.63	Smith and Jungers, 1997	Polygynous	Both
Cercopithecus_lhoesti	5.970	3.450	1.73	Smith and Jungers, 1997	Polygynous	Terrestrial
Cercopithecus_mitis	7.930	4.250	1.87	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_mona	4.780	3.700	1.29	Rowe and Myers, 2017	Polygynous	Arboreal
Cercopithecus_neglectus	7.350	4.130	1.78	Smith and Jungers, 1997	Polygynous	Both
Cercopithecus_nictitans	6.670	4.260	1.57	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_petaurista	4.400	2.900	1.52	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_pogonias	4.260	2.900	1.47	Smith and Jungers, 1997	Polygynous	Arboreal
Cercopithecus_preussi	4.700	2.900	1.62	Rowe and Myers, 2017	Polygynous	Terrestrial

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Cercopithecus_solatus	6.890	3.920	1.76	Smith and Jungers, 1997	Polygynous	Both
Cercopithecus_wolfi	3.910	2.870	1.36	Smith and Jungers, 1997	Polygynous	Arboreal
Cheirogaleus_major	0.440	0.360	1.22	Smith and Jungers, 1997	Monogamous	Arboreal
Cheirogaleus_medius	0.120	0.140	0.86	Rowe and Myers, 2017	Monogamous	Arboreal
Cheracebus_lugens	1.050	1.150	0.91	Rowe and Myers, 2017	Monogamous	Arboreal
Cheracebus_torquatus	1.280	1.210	1.06	Smith and Jungers, 1997	Monogamous	Arboreal
Chiropotes_albinasus	3.150	2.490	1.27	Smith and Jungers, 1997	Polygynandrous	Arboreal
Chiropotes_chiropotes	2.900	2.580	1.12	Smith and Jungers, 1997	Polygynandrous	Arboreal
Chiropotes_satanas	3.100	2.960	1.05	Smith and Jungers, 1997	Polygynandrous	Arboreal
Chlorocebus_aethiops	5.300	3.300	1.61	Smith and Jungers, 1997	Polygynous	Terrestrial
Chlorocebus_cynosuros	6.400	4.900	1.31	Rowe and Myers, 2017	Polygynandrous	Terrestrial
Chlorocebus_pygerythrus	4.130	2.570	1.61	Rowe and Myers, 2017	Polygynandrous	Terrestrial
Chlorocebus_sabaeus	6.300	4.400	1.43	Rowe and Myers, 2017	Polygynous	Terrestrial
Chlorocebus_tantalus	6.400	4.900	1.31	Rowe and Myers, 2017	Polygynandrous	Terrestrial
Colobus_angolensis	9.680	7.570	1.28	Smith and Jungers, 1997	Polygynous	Arboreal
Colobus_guereza	13.500	9.200	1.47	Smith and Jungers, 1997	Polygynous	Arboreal
Colobus_polykomos	9.900	8.300	1.19	Smith and Jungers, 1997	Polygynous	Arboreal
Colobus_satanas	10.400	7.420	1.40	Smith and Jungers, 1997	Polygynous	Arboreal
Colobus_vellerosus	8.500	6.900	1.23	Smith and Jungers, 1997	Polygynous	Arboreal
Daubentonia_madagascariensis	2.620	2.490	1.05	Smith and Jungers, 1997	Polygynandrous	Arboreal
Erythrocebus_patas	12.400	6.500	1.91	Smith and Jungers, 1997	Polygynous	Terrestrial
Eulemur_albifrons	2.210	2.150	1.03	Rowe and Myers, 2017	-	Arboreal
Eulemur_cinereiceps	2.190	2.140	1.02	Rowe and Myers, 2017	-	Arboreal
Eulemur_coronatus	1.280	1.080	1.19	Smith and Jungers, 1997	Polygynous	Arboreal
Eulemur_flavifrons	2.320	2.290	1.01	Rowe and Myers, 2017	Polygynous	Arboreal
Eulemur_fulvus	1.870	1.780	1.05	Smith and Jungers, 1997	-	Arboreal
Eulemur_macaco	2.370	2.510	0.94	Smith and Jungers, 1997	Polygynandrous	Arboreal
Eulemur_mongoz	1.410	1.560	0.90	Smith and Jungers, 1997	Monogamous	Arboreal
Eulemur_rubriventer	1.980	1.940	1.02	Smith and Jungers, 1997	Monogamous	Arboreal
Eulemur_rufifrons	2.180	2.250	0.97	Rowe and Myers, 2017	-	Arboreal
Eulemur_rufus	1.790	1.840	0.97	Rowe and Myers, 2017	Polygynous	Arboreal
Euoticus_elegantulus	0.290	0.260	1.12	Smith and Jungers, 1997	Polygynous	Arboreal
Galago_alleni	0.280	0.270	1.04	Smith and Jungers, 1997	Polygynous	Arboreal
Galago_matschiei	0.210	0.210	1.00	Smith and Jungers, 1997	-	Arboreal

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Galago_moholi	0.190	0.170	1.12	Smith and Jungers, 1997	Polygynous	Arboreal
Galago_senegalensis	0.310	0.250	1.24	Smith and Jungers, 1997	Polygynous	Arboreal
Galagoides_demidoff	0.060	0.060	1.00	Smith and Jungers, 1997	Polygynous	Arboreal
Galagoides_rondoensis	0.060	0.060	1.00	Rowe and Myers, 2017	-	Arboreal
Galagoides_thomasi	0.080	0.070	1.14	Smith and Jungers, 1997	Polygynandrous	Arboreal
Galagoides_zanzibaricus	0.150	0.140	1.07	Smith and Jungers, 1997	Polygynous	Arboreal
Gorilla_beringei	162.500	97.500	1.67	Smith and Jungers, 1997	Polygynous	Both
Gorilla_gorilla	170.400	71.500	2.38	Smith and Jungers, 1997	Polygynous	Both
Hapalemur_aureus	1.520	1.390	1.09	Smith and Jungers, 1997	Monogamous	Arboreal
Hapalemur_griseus	0.750	0.670	1.12	Smith and Jungers, 1997	Monogamous	Arboreal
Hapalemur_occidentalis	0.846	1.180	0.72	Rowe and Myers, 2017	Monogamous	Arboreal
Homo_sapiens	72.100	62.100	1.16	Smith and Jungers, 1997	-	Terrestrial
Hoolock_hoolock	6.870	6.880	1.00	Smith and Jungers, 1997	Monogamous	Arboreal
Hylobates_agilis	5.880	5.820	1.01	Smith and Jungers, 1997	Monogamous	Arboreal
Hylobates_klossii	5.670	5.920	0.96	Smith and Jungers, 1997	Monogamous	Arboreal
Hylobates_lar	5.900	5.340	1.10	Smith and Jungers, 1997	Monogamous	Arboreal
Hylobates_moloch	6.580	6.250	1.05	Smith and Jungers, 1997	Monogamous	Arboreal
Hylobates_muelleri	5.710	5.350	1.07	Smith and Jungers, 1997	Monogamous	Arboreal
Hylobates_pileatus	5.500	5.440	1.01	Smith and Jungers, 1997	Monogamous	Arboreal
Indri_indri	5.830	6.840	0.85	Smith and Jungers, 1997	Monogamous	Arboreal
Lagothrix_lagotricha	7.280	7.020	1.04	Smith and Jungers, 1997	Polygynandrous	Arboreal
Lagothrix_lugens	8.000	6.000	1.33	Rowe and Myers, 2017	Polygynandrous	Arboreal
Lemur_catta	2.210	2.210	1.00	Smith and Jungers, 1997	Polygynandrous	Both
Leontopithecus_chrysomelas	0.620	0.535	1.16	Smith and Jungers, 1997	Monogamous	Arboreal
Leontopithecus_rosalia	0.620	0.598	1.04	Smith and Jungers, 1997	Monogamous	Arboreal
Lepilemur_aeeclis	0.870	0.910	0.96	Rowe and Myers, 2017	-	Arboreal
Lepilemur_edwardsi	0.910	0.930	0.98	Smith and Jungers, 1997	Monogamous	Arboreal
Lepilemur_leucopus	0.620	0.590	1.05	Smith and Jungers, 1997	Polygynous	Arboreal
Lepilemur_petteri	0.630	0.600	1.05	Rowe and Myers, 2017	-	Arboreal
Lepilemur_ruficaudatus	0.760	0.780	0.97	Smith and Jungers, 1997	Monogamous	Arboreal
Lepilemur_sahamalazensis	0.700	0.680	1.03	Rowe and Myers, 2017	-	Arboreal
Lophocebus_albigena	8.250	6.020	1.37	Smith and Jungers, 1997	Polygynandrous	Arboreal
Lophocebus_aterrimus	7.840	5.760	1.36	Smith and Jungers, 1997	Polygynandrous	Arboreal
Loris_lydekkerianus	0.210	0.180	1.17	Rowe and Myers, 2017	Polygynandrous	Arboreal

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Loris_tardigradus	0.160	0.130	1.23	Rowe and Myers, 2017	-	Arboreal
Macaca_arctoides	12.200	8.400	1.45	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_assamensis	11.300	6.900	1.64	Smith and Jungers, 1997	Polygynandrous	Arboreal
Macaca_cyclopis	6.000	4.940	1.21	Smith and Jungers, 1997	Polygynous	Both
Macaca_fascicularis	5.360	3.590	1.49	Smith and Jungers, 1997	Polygynandrous	Arboreal
Macaca_fuscata	11.000	8.030	1.37	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_hecki	11.200	6.800	1.65	Rowe and Myers, 2017	Polygynandrous	Arboreal
Macaca_leonina	7.700	4.900	1.57	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_maura	9.720	6.050	1.61	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_mulatta	7.710	5.370	1.44	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_nemestrina	11.200	6.500	1.72	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_nigra	9.890	5.470	1.81	Smith and Jungers, 1997	Polygynandrous	Terrestrial
Macaca_nigrescens	5.800	5.500	1.05	Rowe and Myers, 2017	Polygynandrous	Arboreal
Macaca_ochreata	5.300	2.600	2.04	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_pagensis	7.000	4.500	1.56	Delson et al., 2000	Polygynandrous	Both
Macaca_radiata	6.670	3.850	1.73	Smith and Jungers, 1997	Polygynandrous	Both
Macaca_silenus	8.900	6.100	1.46	Rowe and Myers, 2017	Polygynous	Arboreal
Macaca_sinica	5.240	3.070	1.71	Rowe and Myers, 2017	Polygynandrous	Arboreal
Macaca_sylvanus	15.300	10.200	1.50	Rowe and Myers, 2017	Polygynandrous	Both
Macaca_thibetana	15.200	9.500	1.60	Smith and Jungers, 1997	Polygynandrous	Terrestrial
Macaca_tonkeana	14.900	9.000	1.66	Smith and Jungers, 1997	Polygynandrous	Both
Mandrillus_leucophaeus	17.500	12.500	1.40	Smith and Jungers, 1997	Polygynous	Both
Mandrillus_sphinx	31.600	12.900	2.45	Smith and Jungers, 1997	Polygynous	Terrestrial
Microcebus_berthae	0.030	0.030	1.00	Rowe and Myers, 2017	Polygynandrous	Arboreal
Microcebus_bongolavensis	0.054	0.054	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_danfossi	0.061	0.066	0.92	Rowe and Myers, 2017	-	Arboreal
Microcebus_gerpi	0.070	0.070	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_griseorufus	0.050	0.060	0.83	Rowe and Myers, 2017	-	Arboreal
Microcebus_jollyae	0.060	0.060	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_lehilahytsara	0.050	0.050	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_macarthurii	0.053	0.053	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_mamiratra	0.060	0.060	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_margotmarshae	0.041	0.041	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_murinus	0.060	0.060	1.00	Smith and Jungers, 1997	Polygynous	Arboreal

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Microcebus_myoxinus	0.030	0.030	1.00	Smith and Jungers, 1997	Polygynandrous	Arboreal
Microcebus_ravelobensis	0.051	0.058	0.88	Rowe and Myers, 2017	-	Arboreal
Microcebus_rufus	0.040	0.043	0.93	Smith and Jungers, 1997	Polygynous	Arboreal
Microcebus_sambiranensis	0.044	0.044	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_simmonsi	0.075	0.075	1.00	Rowe and Myers, 2017	-	Arboreal
Microcebus_tavaratra	0.061	0.061	1.00	Rowe and Myers, 2017	-	Arboreal
Miopithecus_talapoin	1.380	1.120	1.23	Smith and Jungers, 1997	Polygynandrous	Both
Mirza_coquereli	0.300	0.330	0.91	Smith and Jungers, 1997	-	Arboreal
Mirza_zaza	0.287	0.299	0.96	Rowe and Myers, 2017	-	Arboreal
Nasalis_larvatus	20.400	9.820	2.08	Smith and Jungers, 1997	Polygynous	Arboreal
Nomascus_hainanus	6.610	6.560	1.01	Rowe and Myers, 2017	Polygynous	Arboreal
Nomascus_leucogenys	6.440	6.600	0.98	Rowe and Myers, 2017	Monogamous	Arboreal
Nomascus_siki	6.570	7.860	0.84	Rowe and Myers, 2017	Monogamous	Arboreal
Nycticebus_bengalensis	1.100	1.020	1.08	Rowe and Myers, 2017	Polygynandrous	Arboreal
Nycticebus_coucang	0.680	0.630	1.08	Rowe and Myers, 2017	-	Arboreal
Nycticebus_javanicus	0.690	0.630	1.10	Rowe and Myers, 2017	-	Arboreal
Nycticebus_pygmaeus	0.420	0.420	1.00	Rowe and Myers, 2017	Polygynous	Arboreal
Otolemur_crassicaudatus	1.190	1.110	1.07	Smith and Jungers, 1997	Polygynandrous	Arboreal
Otolemur_garnettii	0.790	0.730	1.08	Smith and Jungers, 1997	Polygynandrous	Arboreal
Pan_paniscus	45.000	33.200	1.36	Smith and Jungers, 1997	Polygynandrous	Both
Pan_troglodytes	42.700	33.700	1.27	Smith and Jungers, 1997	Polygynandrous	Both
Papio_anubis	25.100	13.300	1.89	Smith and Jungers, 1997	Polygynandrous	Terrestrial
Papio_cynocephalus	22.500	12.400	1.81	Rogers et al. 2019	Polygynandrous	Terrestrial
Papio_hamadryas	20.900	12.000	1.74	Rogers et al. 2019	Polygynous	Terrestrial
Papio_kindae	16.000	10.300	1.55	Rogers et al. 2019	Polygynandrous	Terrestrial
Papio_papio	20.200	11.800	1.71	Rogers et al. 2019	Polygynous	Terrestrial
Papio_ursinus	28.100	15.900	1.77	Rogers et al. 2019	Polygynandrous	Terrestrial
Perodicticus_potto	1.500	1.570	0.96	Rowe and Myers, 2017	Monogamous	Arboreal
Phaner_pallescens	0.330	0.350	0.94	Rowe and Myers, 2017	Monogamous	Arboreal
Piliocolobus_badius	8.360	8.210	1.02	Rowe and Myers, 2017	Polygynandrous	Arboreal
Piliocolobus_kirkii	5.800	5.460	1.06	Rowe and Myers, 2017	Polygynandrous	Arboreal
Piliocolobus_pennantii	11.000	10.000	1.10	Rowe and Myers, 2017	Polygynous	Arboreal
Piliocolobus_preussi	8.300	7.300	1.14	Rowe and Myers, 2017	Polygynandrous	Arboreal
Piliocolobus_rufomitratus	9.670	7.210	1.34	Rowe and Myers, 2017	Polygynous	Arboreal

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Piliocolobus_tephrosceles	10.500	7.000	1.50	Rowe and Myers, 2017	Polygynandrous	Arboreal
Pithecia_irrorata	2.250	2.070	1.09	Smith and Jungers, 1997	-	Arboreal
Pithecia_monachus	2.610	2.110	1.24	Smith and Jungers, 1997	Monogamous	Arboreal
Pithecia_pithecia	1.940	1.580	1.23	Smith and Jungers, 1997	Monogamous	Arboreal
Plecturocebus_brunneus	0.850	0.800	1.06	Smith and Jungers, 1997	Monogamous	Arboreal
Plecturocebus_cupreus	1.020	1.120	0.91	Smith and Jungers, 1997	Monogamous	Arboreal
Plecturocebus_donacophilus	0.991	0.909	1.09	Smith and Jungers, 1997	Monogamous	Arboreal
Plecturocebus_hoffmannsi	1.090	1.030	1.06	Smith and Jungers, 1997	-	Arboreal
Plecturocebus_moloch	1.020	0.960	1.06	Smith and Jungers, 1997	-	Arboreal
Pongo_abelii	77.900	35.600	2.19	Smith and Jungers, 1997	Polygynandrous	Arboreal
Pongo_pygmaeus	78.500	35.800	2.19	Smith and Jungers, 1997	Polygynous	Arboreal
Presbytis_chrysomelas	6.550	6.900	0.95	Delson et al., 2000	Polygynous	Arboreal
Presbytis_comata	6.680	6.710	1.00	Smith and Jungers, 1997	-	Arboreal
Presbytis_femoralis	6.260	6.190	1.01	Smith and Jungers, 1997	Polygynous	Arboreal
Presbytis_frontata	5.560	5.670	0.98	Smith and Jungers, 1997	Polygynous	Arboreal
Presbytis_hosei	6.180	5.630	1.10	Smith and Jungers, 1997	Polygynous	Arboreal
Presbytis_melalophos	6.590	6.470	1.02	Smith and Jungers, 1997	Polygynous	Arboreal
Presbytis_potenziani	6.170	6.400	0.96	Smith and Jungers, 1997	Polygynous	Arboreal
Presbytis_rubicunda	6.290	6.170	1.02	Smith and Jungers, 1997	Polygynous	Arboreal
Presbytis_thomasi	6.770	6.690	1.01	Smith and Jungers, 1997	-	Arboreal
Procolobus_verus	4.700	4.200	1.12	Smith and Jungers, 1997	Polygynous	Arboreal
Prolemur_simus	2.240	2.250	1.00	Rowe and Myers, 2017	Polygynous	Arboreal
Propithecus_coquereli	3.700	4.280	0.86	Rowe and Myers, 2017	Polyandrous	Arboreal
Propithecus_deckenii	2.930	2.630	1.11	Rowe and Myers, 2017	-	Arboreal
Propithecus_diadema	5.940	6.260	0.95	Smith and Jungers, 1997	Polygynous	Arboreal
Propithecus_edwardsi	5.500	5.700	0.96	Rowe and Myers, 2017	Monogamous	Arboreal
Propithecus_perrieri	4.700	4.500	1.04	Rowe and Myers, 2017	-	Arboreal
Propithecus_tattersalli	3.390	3.590	0.94	Smith and Jungers, 1997	-	Arboreal
Propithecus_verreauxi	3.250	2.950	1.10	Smith and Jungers, 1997	Polygynous	Arboreal
Pygathrix_cinerea	11.500	8.450	1.36	Rowe and Myers, 2017	Polygynandrous	Arboreal
Pygathrix_nemaeus	11.000	8.440	1.30	Smith and Jungers, 1997	Polygynous	Arboreal
Pygathrix_nigripes	11.000	9.000	1.22	Rowe and Myers, 2017	Polygynandrous	Arboreal
Rhinopithecus_avunculus	14.000	8.500	1.65	Smith and Jungers, 1997	Polygynous	Arboreal
Rhinopithecus_bieti	15.000	9.960	1.51	Smith and Jungers, 1997	Polygynous	Both

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Rhinopithecus_brelichi	15.000	8.000	1.87	Rowe and Myers, 2017	Polygynous	Both
Rhinopithecus_roxellana	17.900	11.600	1.54	Smith and Jungers, 1997	Polygynous	Both
Rhinopithecus_strykeri	14.000	8.500	1.65	Rowe and Myers, 2017	-	Both
Saguinus_bicolor	0.428	0.430	1.00	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_fuscicollis	0.343	0.358	0.96	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_geoffroyi	0.400	0.500	0.80	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_imperator	0.474	0.475	1.00	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_inustus	0.585	0.803	0.73	Smith and Jungers, 1997	-	Arboreal
Saguinus_labiatus	0.490	0.529	0.93	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_leucopus	0.494	0.490	1.01	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_midas	0.515	0.575	0.90	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_mystax	0.510	0.540	0.94	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_niger	0.474	0.505	0.94	Rowe and Myers, 2017	Polyandrous	Arboreal
Saguinus_nigricollis	0.468	0.484	0.97	Smith and Jungers, 1997	Polyandrous	Arboreal
Saguinus_oedipus	0.420	0.400	1.05	Smith and Jungers, 1997	Monogamous	Arboreal
Saimiri_boliviensis	0.911	0.711	1.28	Smith and Jungers, 1997	Polygynandrous	Arboreal
Saimiri_oerstedii	0.897	0.680	1.32	Smith and Jungers, 1997	Polygynandrous	Arboreal
Saimiri_sciureus	0.779	0.662	1.18	Smith and Jungers, 1997	Polygynandrous	Arboreal
Saimiri_ustus	0.920	0.799	1.15	Smith and Jungers, 1997	-	Arboreal
Sapajus_apella	3.900	3.000	1.30	Rowe and Myers, 2017	-	Arboreal
Sapajus_libidinosus	3.100	1.975	1.57	Rowe and Myers, 2017	Polygynandrous	Arboreal
Semnopithecus_entellus	13.000	9.890	1.31	Smith and Jungers, 1997	Polygynous	Terrestrial
Semnopithecus_hector	18.000	15.000	1.20	Rowe and Myers, 2017	Polygynandrous	Both
Semnopithecus_priam	11.400	6.910	1.65	Smith and Jungers, 1997	Polygynous	Terrestrial
Simias_concolor	9.150	6.800	1.35	Smith and Jungers, 1997	Polygynous	Both
Symphalangus_syndactylus	11.900	10.700	1.11	Smith and Jungers, 1997	Monogamous	Arboreal
Tarsius_bancanus	0.128	0.117	1.09	Rowe and Myers, 2017	Polygynous	Arboreal
Tarsius_fuscus	0.129	0.119	1.08	Rowe and Myers, 2017	Monogamous	Arboreal
Tarsius_lariang	0.118	0.102	1.16	Rowe and Myers, 2017	Monogamous	Arboreal
Tarsius_sangirensis	0.135	0.150	0.90	Rowe and Myers, 2017	-	Arboreal
Tarsius_tarsier	0.136	0.119	1.14	Rowe and Myers, 2017	Monogamous	Arboreal
Tarsius_wallacei	0.115	0.099	1.16	Rowe and Myers, 2017	-	Arboreal
Theropithecus_gelada	19.000	11.700	1.62	Smith and Jungers, 1997	Polygynous	Terrestrial
Trachypithecus_auratus	6.600	5.700	1.16	Smith and Jungers, 1997	Polygynous	Arboreal

Species	Male body mass (kg)	Female body mass (kg)	Sexual Size Dimorphism	Body mass source	Mating system (Rowe and Myers, 2017)	Terrestriality (Gallen-acedo et al., 2019)
Trachypithecus_barbei	7.100	5.700	1.25	Rowe and Myers, 2017	Polygynous	-
Trachypithecus_cristatus	6.610	5.760	1.15	Smith and Jungers, 1997	Polygynous	Arboreal
Trachypithecus_delacouri	8.600	7.800	1.10	Rowe and Myers, 2017	Polygynous	Both
Trachypithecus_francoisi	7.700	7.350	1.05	Smith and Jungers, 1997	Polygynous	Both
Trachypithecus_geei	10.800	9.500	1.14	Smith and Jungers, 1997	Polygynous	Arboreal
Trachypithecus_germaini	6.500	7.000	0.93	Rowe and Myers, 2017	Polygynandrous	Arboreal
Trachypithecus_hatinhensis	8.450	7.200	1.17	Rowe and Myers, 2017	Polygynous	Both
Trachypithecus_johnii	12.000	11.200	1.07	Smith and Jungers, 1997	Polygynous	Arboreal
Trachypithecus_laotum	8.000	7.000	1.14	Rowe and Myers, 2017	Polygynous	Both
Trachypithecus_obscurus	7.900	6.260	1.26	Smith and Jungers, 1997	Polygynous	Arboreal
Trachypithecus_phayrei	7.870	6.300	1.25	Smith and Jungers, 1997	Polygynous	Arboreal
Trachypithecus_pileatus	12.000	9.860	1.22	Smith and Jungers, 1997	Polygynous	Arboreal
Trachypithecus_poliocephalus	9.500	8.000	1.19	Rowe and Myers, 2017	Polygynous	Both
Trachypithecus_shortridgei	13.200	9.550	1.38	Delson et al., 2000	Polygynous	Arboreal
Trachypithecus_vetulus	8.170	5.900	1.38	Smith and Jungers, 1997	-	Arboreal
Varecia_rubra	3.550	3.470	1.02	Rowe and Myers, 2017	Polyandrous	Arboreal
Varecia_variegata	3.630	3.520	1.03	Rowe and Myers, 2017	Polyandrous	Arboreal