Sexual Dimorphism in Primates

FJ McPherson*
School of Agriculture and Wine Science, Charles Sturt University, Wagga Wagga, NSW 2650 Australia

There are almost 5000 species of mammals existing today including 129 species of prosimians, 264 species of monkeys, 17 species of gibbons (‘lesser apes’) and 7 species of great apes including humans [1]. All primates reproduce sexually which has led to the evolution of sexual differentiation and Sexual Dimorphism (SD) in terms of behavior, body size, pelage, anatomy and vocalization.

Selection pressures on male mammals are often greater than on females which have meant males have developed more accentuated features. In many species, polygynous social structure means that only a few males will be able to reproduce compared with females which rarely fail to reproduce at least once and this is linked to the development of SD [2]. In primates such as baboons, adult males are more likely than females to confront predators which could further explain the evolution of exaggerated male sexual secondary characteristics (SSC) such as enlarged canine teeth [3]. Males with exaggerated SSC also benefit the most in terms of access to estrous females and therefore reproductive success compared to males with less exaggerated SSC [4]. Japanese macaques (Macaca fuscata) are an exception as male mates are chosen not based on social ranking but on each female macaque’s own interpretation of male attractiveness. Thus some offspring can be sired by subordinate males even though dominant males are available [5].

One explanation for greater body size in one sex could be uneven selection pressures on the sexes [4,6] while a more rapid growth rate (Hypothesis A) or a different length in growth period for males and females (Hypothesis B) can also account for body size SD. Male talapo in monkeys (Miopithecus talapoin) are an example of Hypothesis A whereas four species of monkey including the Sulawesi macaque (Macaca nigra) and the douc langur (Pygathrix nemaeus) are examples of Hypothesis B [6]. Generally males are larger than females although the degree to which they differ depends on the species, captive or wild status and their age, among other factors. The greatest body size dimorphism is generally displayed by primates in polygynous mating groups [2]. When males are competing against other males in neighbouring troops due to overlapping home ranges, body size SD can be increased as is the case with Asian Colobine primates [7]. However, when primates, especially great apes, are kept in captivity, there may be great exaggeration in body size SD compared to their wild counterparts. This is due to captivity resulting in obesity due to restrictions on foraging and lack of exercise [8]. Thus, phenotypic and quantitative traits are influenced more by domestication rather than selection pressure [9]. Captive male great apes, regardless of dominance ranking, tend to attain much greater body size SD than they would display in the wild where non-dominant males and adult females are of similar size [10].

Another striking example of dimorphism involves the canine teeth. Gelada baboon (Theropithecus gelada) adult males possess canine teeth which are 3.5 times longer than those of females [6]. While canine teeth SD is present in simians, following the same trend as body size SD in New World monkeys [11], it is generally lacking in prosimians such as lemurs, lorises and tarsiers [6]. Canine teeth serve to protect against predators, warn individuals to prevent fighting as well as sexual selection of mates. Diurnal species show greater canine teeth SD than nocturnal species, presumably because such visual displays are more effective during daylight hours. Terrestrial primates tend to have greater canine teeth SD than primates which are mainly arboreal, which could be related to the more frequent threats of predation for terrestrial species [12].

Behaviours can be sex-specific although it would be misleading to automatically assume that individuals with offspring are female. This is because in many primate species, both parents are actively involved in rearing their single or twin offspring. Some examples of such attendant monomorphic males are the saddle-back tamarin (Sanguinus fusicollis), common marmoset (Callithrix jacchus) and cottontop marmoset (Saguinus oedipus) [13].

Sexual dichromatism is present in mammals although not to as great an extent as in avian species [14]. Usually the males are more brightly colored than their female counterparts which could provide a visual clue as to male reproductives fitness when females select partners based on colour [15]. An experiment involving captive common brown lemur (Eulemur fulvus) showed that females spent significantly more time looking at photographs of brightly male lemur faces compared to photographs of less brightly colored male lemur faces [14] which confirms that male selection for females is based on pelage color in E. fulvus. An obvious example of sexual dichromatism occurs in Howler monkeys (Alouatta caraya) where the male is jet black and the female is a beige colour. Likewise, mature male gorillas (Gorilla gorilla) develop a silver-haired ‘saddle’ which the entirely black females and immature males lack [16]. In the latter examples, it is possible to tell the sexes apart from a distance but pelage differences can also be subtle. For example, only adult female Squirrel monkeys (Saimiri sciureus) over 5 years of age have a small black patch on each side of the head anterior to the ear [17]. Another example of pelage SD is the presence of a thick mane in adult males of some species such as Hamadryas baboons (Papio hamadryas) which serves as a sexual selection aid for females as well as a protective function for the males during physical conflicts [6].

Skin color can be subject to SD also as in the case of male Mandrills (Papio sphinx) which have vividly colored rumps and noses compared to the females, possibly to signal reproductive fitness and/or dominance [14,18,19]. Although there is no difference in skin color between the sexes, only adult male orange uandesvelop cheek flanges [20].

Sexual dimorphism in vocalization can be related to selection of mates and territoriality. The honking sounds produced by male

*Corresponding author: FJ McPherson, School of Agriculture and Wine Science, Charles Sturt University, Wagga Wagga, NSW 2650 Australia, E-mail: fmcpherson@csu. edu. au

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proboscis monkeys (*Nasalis larvatus*) are much louder than those made by the females because the males have a much larger nose which fills with blood to amplify the warning sounds. Similarly, male howler monkeys have much larger inflatable throat sacs than females which serve to amplify their calls [20]. In a further adaptation, male howlers, but not females, have bony resonators due to hyoid bone modifications to aid with sound amplification [21].

Three forms of vocal SD are present in primates due to specific male or female roles. Male calls serve to keep neighbouring troops away while females call to either solicit mating [22] or affirm their pair-bond as in gibbons and howlers [23]. One example is phonation discrepancy as in Guenon monkeys (*Cercopithecus spp*) while another example of vocal SD is the differential production in shared call types. Examples of the latter include gibbons (*Hylobates spp*), gorilla (*G. gorilla*), chimpanzees (*Pan troglodytes*) and vervet monkeys (*Chlorocebus spp*). There are also sex-specific call types as in red-capped Mangebeys (*Cercocebus torquatus*). Monomorphic species such as marmosets and tamarins, can display vocalization SD as is the case with female cotton-top tamarins (*Saguinus oedipus*). There are also sex-specific call types in red-capped Mangebeys (*Cercocebus torquatus*). Monomorphic species such as marmosets and tamarins, can display vocalization SD as is the case with female cotton-top tamarins (*Saguinus oedipus*) which vocalize more than males [23].

**References**