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Original Article

Are badges of status adaptive in large complex primate groups?

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ABSTRACT

Sexual dimorphism in ornamentation in primates may have been sexually selected as signals of rank and dominance to males or by augmenting attractiveness to females. While male primates display tremendous variation in secondary sexual traits, such as sexual skin, capes of hair, and beards, which are often attributed to sexual selection, their phylogenetic distribution remains to be fully understood. Here we investigate the hypothesis that sexual dimorphism in ornaments is more pronounced in larger more 'anonymous' social organizations where quick reliable assessment of male quality, social status, dominance, and aggressiveness are selective pressures. Multiple regression analyses, including phylogenetic correction, were performed on 154 species representing 45 genera of simian primates. We found a positive relationship between degree of ornamental dimorphism and group size, even after controlling for other independent variables such as habitat type (i.e. openness of terrain) and fission–fusion dynamics. Dimorphism was also significantly associated with social organization, so that males from species with multilevel social organizations had the highest ratings for ornamentation. In sum, our analysis suggests that among primates with larger group sizes and multilevel social organizations, males have more developed visually conspicuous secondary sexual traits. This may reflect selection for amplified signals of individual identity, rank, dominance, or attractiveness in large and complex social organizations wherein social and physical conflict may arise frequently and individual recognition is limited.

1. Introduction

Male primates express a diverse array of conspicuous colorful, hairy, and fleshy traits. Their marked sexual dimorphism strongly suggests a role of sexual selection in their origins, either as badges of status or attractive ornaments (Andersson, 1994; Darwin, 1871). Examples include the elongated noses in proboscis monkeys (*Nasalis larvatus*), cheek flanges in orang-utans (*Pongo* spp.), capes of white and silvery-grey hair in hamadryas baboons (*Papio hamadryas*), reddened chests in geladas (*Theropithecus gelada*), upper-lip warts in golden snub-nosed monkeys (*Rhinopithecus roxellana*), and beards in humans (*Homo sapiens*; Dixson, Dixson, & Anderson, 2005).

At least some of these ornaments may enhance male sexual attractiveness to females (Dixson, 2012). Female Bornean orang-utans, for example, mate more often with males with fully developed cheek-flanges than un-flanged males around ovulation (Knott, Thompson, Stumpf, & McIntyre, 2010). Red and blue coloration in the mandrill (*Mandrillus sphinx*) may advertise genetic diversity around the MHC (Setchell, Charpentier, Abbott, Wickings, & Knapp, 2010; Setchell & Huchard, 2010). The red skin that covers the head and face in the red uakari (*Cacajao calvus*) becomes paler during times of sickness, suggesting that disease may affect the expression of male ornamentation (Nunn & Altizer, 2006). Male rhesus macaques (*Macaca mulatta*) with darker red facial coloration receive more sexual solicitations from a greater number of females during the mating season than paler faced males (Dubuc, Allen, Maestripieri, & Higham, 2014). However, many factors affect male mating success and it remains to be demonstrated among other species whether mating success is determined by the attractiveness of secondary sexual ornaments and whether male ornaments associated with genetic benefits enhance sexual attractiveness.

Pronounced sexual dimorphism in body mass and canine size has been well documented in male primates (Plavcan, 2012) and is functionally linked to the frequency and intensity of male competition (Grueter & van Schaik, 2009; Plavcan & van Schaik, 1992, 1997). There is mounting evidence that visually conspicuous adornments serve as badges of status, signalling dominance rank within sexes (Dixson, 2012). Such ornaments function in concert with body size during male–male agonistic interactions, where cues that signal strength and fighting ability to conspecific competitors may serve to curtail the probability of conflicts escalating into fights (Barrette & Vandal, 1990; Maynard-Smith, 1982). Mature male western gorillas (*Gorilla gorilla*) have more muscle mass and are larger than females, with silvery gray hair on their backs and a bony-adipose crest on top of the head. Males with the largest adipose crests have the most females in their one-male units (Caillaud, Levréro, Gatti, Ménard, & Raymond, 2008) and crest size is significantly correlated with offspring survival and the annual rate of siring offspring that survive to weaning age (Breuer, Robbins, Boesch, & Robbins, 2012). The expression of fully developed

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cheek flanges and beards in male orang-utans depends on gaining dominant status (Galdikas, 1985; Kingsley, 1982; Utami Atmoko & van Hooff, 2004). Red facial coloration in male mandrills is positively associated with social dominance (Setchell & Dixson, 2001a; Wickings & Dixson, 1992), with gain of higher social rank (Setchell & Dixson, 2001b), and reproductive success (Wickings & Dixson, 1992). Similarly, male drills (*Mandrillus leucophaeus*) can be up to three times the size of females, possess large canines, and marked sexual dimorphism in coloration. Brightness of male ornaments correlates with greater dominance rank and reproductive success (Marty, Higham, Gadsby, & Ross, 2009). The redness of the skin patch on the chest of male geladas is also brighter among those males with larger harems, whereas bachelor and secondary follower males have more muted coloration (Bergman, Ho, & Beehner, 2009).

Primates live in diverse social organizations that differ markedly in their sizes and composition. The strength of conspicuous ornaments in conveying male rank, dominance, and social status may vary depending on the composition and size of the social group. The functional value of such ornaments is expected to be particularly high in large and fluid groups in which social knowledge is limited (Bergman, 2010; Bergman & Sheehan, 2013; Bergman et al., 2009; Marty et al., 2009; Setchell & Kappeler, 2003). For example, male mandrills spend long periods of time in isolation before joining large hordes of females after they have entered tumescence (Abernethy, White, & Wickings, 2002). In such a scenario where males do not develop long-term bonds between social or breeding partners, the evolution of highly conspicuous signals of male rank and dominance may facilitate rapid recognition of male dominance, rank, and status involved in intra-sexual competition and possibly female choice (Dixson, 2012). Among geladas and hamadryas baboons, both of which live in multilevel polygynous societies wherein one-male units are part of higher-level social groupings and in frequent contact, sexual selection may have shaped the evolution of conspicuous signals of rank and dominance (Bergman & Sheehan, 2013; Bergman et al., 2009). Conversely, in smaller cohesive groups, individual recognition and more frequent interactions may allow animals to better assess the social status, strength, and quality of their contemporaries and potentially reduce the selective pressures for external ornaments (Kappeler & van Schaik, 2004). Thus, among species that exist in larger social groups, ornaments may be better developed than among smaller groups. Indeed, recent comparative analyses reported a positive correlation between group size and complexity of facial color patterns in Old Word monkeys and apes (Catarrhini; Santana, Alfaro, Noonan, & Alfaro, 2013). The catarrhines differ from New World monkeys (Platyrrhini), where color patterns have evolved to facilitate individual recognition in small social groups (Santana et al., 2013). Further, Old Word monkeys that are highly gregarious and sympatric express more complex facial color patterns than species characterized by non-gregarious and non-sympatric social organizations (Santana et al., 2013), as do New World monkeys living in small social groups with high levels of sympatry (Santana, Alfaro, & Alfaro, 2012).

The properties of the environment and the risk of predation may also impact on the expression of ornamentation between species. In guppies (*Poecilia reticulata*), while male coloration is under strong sexual selection via female choice (Houde, 1997), polymorphisms in ornamental color patterns between populations might reflect a compromise between conspicuously signalling attractiveness and crypsis (Endler, 2000). In agamid lizards, concealed sexually dichromatic ornaments are better developed among species living in closed than open habitats (Stuart–Fox & Ord, 2004). Primates also occupy variable habitats, from open savannahs to densely forested areas and the intensity of coloration may be inversely related to darkness of the environment (Chaplin & Jablonski, 1998; see also Marchetti, 1993). Interestingly, catarrhines that live in more densely forested and humid habitats have more darkly pigmented faces (Santana et al., 2013). Kamilar and Bradley (2011) also found a positive effect of evotranspiration on pelage darkness across primates. Thus, in addition to social structure, ecological factors are associated with diversity in the complexity of color patterning in facial ornaments and pelage among primates.

Despite mounting evidence that among male primates secondary sexual traits serve as ornaments that attract females and as badges of status between males, their phylogenetic distribution remains to be fully understood. In the present study we employ a quantitative measure of sexual dimorphism in ornamentation, including all hairy, fleshy, and colorful adornments, in a cross-species comparative approach to assess the evolution of ornamentation in male primates. We analyzed phylogenetic regression models using data from simian primates representing 154 species from 45 genera. We base our predictions on the theory that male–male competition and female choice have shaped the evolution of visually conspicuous sexually dimorphic traits in male primates. Recent comparative evidence reveals that facial color patterning is more complex among catarrhines living in larger and more sympatric social groups (Santana et al., 2013; see also Allen, Stevens, & Higham, 2014). Thus, we use group size as a proxy for the degree of 'social anonymity' (Bergman et al., 2009; Moffett, 2013) and predicted that the selective pressures for signalling status to male conspecifics and attractiveness to females result in greater male ornamentation in species with larger group sizes. There is also evidence that individuals in larger groups spread out as a counterstrategy to scramble competition (e.g. Snaith & Chapman, 2008), thus exacerbating the perceived level of 'anonymity'. Further, the social composition of the group and the extent to which species exhibit fission–fusion dynamics characterized by frequent flux in group membership may put a premium on readily apparent signals of rank, dominance, and attractiveness. The degree to which each species exhibits group cohesion both over long and short timescales was included in the model as a possible contributing factor influencing ornamentation. We also included habitat type as a potential factor predicting ornamental diversity across species. Mating system has also been shown to correlate with dimorphism in male visual traits, with polygynous species scoring highest for sexual dimorphism in adornments (Dixson et al., 2005). Here we extend this work to test how social aspects of sexual selection might generate selective pressures for signals of rank and attractiveness. Thus, we included a refined classification of primate social organizations as a predictor variable and tested this against mating systems in our analysis to test the prediction that species with multilevel social organizations have higher scores for ornamentation.

2. Methods

2.1. Quantifying sexual dimorphism in ornaments

Sexual dimorphism in every discernible ornament was quantified using a 6-point rating scale (Dixson et al., 2005), where 0 = no difference between males and females (e.g., both sexes have a crest of hair of the same size and color); 1 = a very slight difference with the visual trait slightly more developed in males than in females; 2 = a small but notable difference in males compared with females; 3 = moderate difference; 4 = large difference between the sexes; 5 = a very large difference (e.g. males possessing a prominent visual trait that is absent, or virtually so, in females). Scores were then summed for a total ornamentation value (range 0–32). All parts had the same weight in the final score. Rating scales of this type have been validated in comparative studies of primate genital morphology (Dixson, 1987; Harcourt & Gardiner, 1994; Verrell, 1992) and visually conspicuous ornaments (Santana et al., 2012, 2013), facilitating statistical and phylogenetic comparisons across a broad spectrum of genera and species.

In the present study ratings for all sexually dimorphic visual traits involving the trunk, limbs, and head for a total of 154 species representing 45 genera of New World monkeys, Old World monkeys and apes, including humans were used. The majority of the data were taken from Dixson et al. (2005) and the dataset was refined and extended to include a few additional species, particularly in the genera *Rhinopithecus*, *Semnopithecus*, *Trachypithecus* and *Cercopithecus*. Scoring was done by