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Sexual Selection and the Differences Between the Sexes in Mandrills (*Mandrillus sphinx*)

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ABSTRACT

Sexual selection has become a major focus in evolutionary and behavioural ecology. It is also a popular research topic in primatology. I use studies of mandrills (*Mandrillus sphinx*), a classic example of extravagant armaments and ornaments in animals, to exemplify how a long-term, multi-disciplinary approach that integrates field observations with laboratory methods can contribute to on-going theoretical debates in the field of sexual selection. I begin with a brief summary of the main concepts of sexual selection theory and the differences between the sexes. I then introduce mandrills and the study population and review mandrill life history, the ontogeny of sex differences, and maternal effects, before focusing on male-male competition and female choice, followed by the less well-studied questions of female-female competition and male choice. This review shows how different reproductive priorities lead to very different life histories and divergent adaptations in males and females. It demonstrates how broadening traditional perspectives on sexual selection beyond the ostentatious results of intense sexual selection on males leads to an understanding of more subtle and cryptic forms of competition and choice in both sexes and opens many productive avenues in the study of primate reproductive strategies. These include the potential for studies of post-copulatory selection, female intra-sexual competition, and male choice. These studies of mandrills provide comparison and, I hope, inspiration for studies of both other polygynandrous species and species with mating systems less traditionally associated with sexual selection.

KEYWORDS

intrasexual competition, mate choice, life history, reproductive strategies, adaptation

INTRODUCTION

How and why the sexes differ in appearance and behaviour is a topic of fascination to evolutionary biologists and lay people alike. First proposed by Darwin in 1859, and elaborated in 1871, sexual selection has become a major focus in evolutionary and behavioural ecology (e.g., Westneat and Fox, 2010). It is also a popular research topic in primatology (Jones, 2003; Kappeler and van Schaik, 2004a; Dixson, 2012). In this article, I use long-term, integrative studies of sexual selection and sex differences in one of the classic examples of extravagant armaments and ornamentation in animals, the mandrill (*Mandrillus*

sphinx), to illustrate developments in the study of sexual selection in primates. I begin with a brief summary of the main concepts of sexual selection theory and the differences between the sexes, highlighting key insights which have expanded our understanding of sexual selection well beyond Darwin's original theory and aspects of sexual selection often not considered in primate research. I then introduce mandrills and the study population. Next, I outline the need for a developmental and long-term perspective in studies of sexual selection, and review mandrill life history, the ontogeny of sex differences and maternal effects on offspring. I then address the components of classical sexual selection theory, male-male competition and female choice, followed by the less well-studied questions of female-female competition and male choice. In each section I outline key theoretical models and debates, review the approaches we have taken to address those questions in mandrills and the results obtained and the implications of these results for our understanding of sexual selection. I also highlight what we do not yet know. I then summarize and synthesize the state of our understanding of sexual selection and sex differences in mandrills, highlighting parallels between males and females as well as fundamental differences in reproductive strategy. Finally, I present future perspectives for the study of sexual selection in mandrills and other primates.

SEXUAL SELECTION AND THE DIFFERENCES BETWEEN THE SEXES

“no other member in the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill” (Darwin, 1871 vol 2, p292).

Darwin originally formulated the theory of sexual selection to account for exaggerated male traits such as the peacock's tail and the Irish elk's antlers, including the 'resplendent' colours of the mandrill (Darwin, 1871 vol 2, p293). These secondary sexual characters (Hunter, 1837) are not directly required for reproduction, unlike primary sexual traits, and pose a challenge to natural selection, as they advertise rather than conceal and are likely to compromise survival. Darwin's insight was that selection will favour traits that increase mating success, even at the cost of a reduction in survival (Darwin, 1871).

Darwin identified two major mechanisms of sexual selection: intrasexual selection and intersexual selection, although he didn't use these terms (Darwin, 1871). Intrasexual selection favours traits that benefit the bearer in competition with members of the same sex for access to mating opportunities, while intersexual selection favours traits that increase the attractiveness of the bearer to members of the opposite sex. Darwin focussed his discussion on male-male contest competition and female choice, although he recognised other

possibilities, including competition between females, male mate choice and the existence of secondary sexual traits in females (Darwin, 1871). This focus on males was later supported by laboratory experiments showing that variance in male mating success (and hence reproductive success) is significantly greater than in females in *Drosophila*, and that reproductive success increases with the number of partners in males, but not in females (Bateman, 1948). Subsequent theory linked these findings to sex differences in parental investment in gametes and parental care (Trivers, 1972), and in the time taken to resume mating activity after fertilisation, and thus potential reproductive rate (Clutton-Brock and Parker, 1992), which lead to biases in the ratio of males and females available to breed at any one time (the operational sex ratio, Emlen and Oring, 1977).

This classical framework of sexual selection set the scene for a great deal of research on sexual selection in males, and abundant support is now available for sexual selection via male-male competition and female choice (Andersson, 1994; Clutton-Brock, 2007). However, it has also become evident that sex differences in reproductive competition and secondary sexual traits are more complex than the classical framework would suggest (Clutton-Brock, 2007). Over time, several key insights have expanded our understanding of sexual selection well beyond the striking visual traits that Darwin sought to explain. These include the implications of polyandrous mating in females, sexual conflict, male choice and female competition.

Although Darwin noted that females of some species mated with multiple partners, he concentrated on what we now term pre-copulatory sexual selection (Birkhead, 2001). The implications of polyandry were neglected until the early 1970s (Parker and Birkhead, 2013; Pizzari and Wedell, 2013). At this point, Parker proposed that mating with multiple males can result in competition for ova during and after copulation, or sperm competition (Parker, 1970) and evidence for sperm preference in *Drosophila* (Childress and Hartl, 1972) led to the concept of cryptic female choice (Thornhill, 1983; Eberhard, 1996). The understanding that both intra- and inter-sexual selection can occur post-insemination in the female reproductive tract opened new avenues and challenges for the study of sexual selection (Birkhead and Pizzari, 2002).

The recognition that females mate polyandrously led to examination of the possible benefits of mating with multiple males, and highlighted the potential for sexual conflict and arms races between the sexes arising from divergence in reproductive priorities between the sexes (Trivers, 1972; Parker, 1979). This can include sexual coercion and sexually-selected infanticide in males, and the evolution of female counter-strategies to these male strategies

(Hrdy, 1974, 1979; Smuts and Smuts, 1993; van Schaik and Janson, 2000; Stumpf et al., 2011; Palombit, 2012). This extends to post-insemination conflict between the sexes, and the spread of sexually antagonistic genes, the expression of which is beneficial to one sex but detrimental to the other (Birkhead and Pizzari, 2002).

In the 1980s, Dewsbury called into question the assumption that male gametes are cheap to produce and, essentially, unlimited (Dewsbury, 1982). This highlighted the potential importance of male choice as a selective force. More recently, several authors have advocated that male mate choice deserves far greater attention than it has received and that mate choice is not as closely tied sex differences in parental investment as previously thought (Clutton-Brock, 2007, 2009; Bonduriansky, 2009; Edward and Chapman, 2011). Instead, mate choice is predicted where the number of mates available exceeds the capacity for mating and where mates vary in quality, a scenario which can apply to both sexes.

Selection during and after, as well as before, copulation and male mate choice fit relatively easily into Darwin's original definition of sexual selection as "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (1871, p256). However, how competition among females fits with the traditional definition of sexual selection is a source of on-going debate. Where females compete for mating opportunities, as in lekking topi antelopes (*Damaliscus lunatus*) (Bro-Jørgensen, 2002), this is unproblematic. However, females are often more limited by access to resources than they are by access to mates, and much of female competition relates to resources that contribute to the number and quality of their offspring (Tobias et al., 2012; Stockley and Campbell, 2013). Here, competition contributes to both reproduction and survival and the boundary between sexual and natural selection becomes blurred (Clutton-Brock, 2009; Stockley and Campbell, 2013). Various proposals have been made for a broader theoretical framework that encompasses both classical sexual selection and female intrasexual competition (West-Eberhard, 1983; Clutton-Brock, 2004, 2007, 2009; Clutton-Brock et al., 2006; Carranza, 2009). West-Eberhard proposes that we view sexual selection as a subset of social selection, which is defined as selection resulting from intra-specific competition for resources (West-Eberhard, 1983). Clutton-Brock argues that we should abandon the distinction between natural and sexual selection and focus on comparing the selection pressures operating on males and females (Clutton-Brock, 2004, 2007, 2009; Clutton-Brock et al., 2006). Carranza suggests that we define sexual selection as sex-dependent selection (Carranza, 2009). If we follow Carranza, then almost all selection in vertebrates can be viewed as sexual selection, although this is not the case for many other organisms (Carranza

2009). Under this interpretation, survival is just one part of an organism's strategy for passing on genes to the next generation, albeit an important one (Carranza, 2009), a scenario intuitively pleasing to students of sexual selection.

MANDRILLS – CREATURES OF EXTREMES

Mandrills are large, terrestrial Cercopithecine monkeys that live in the dense equatorial forest of Central Africa (Grubb, 1973). Although mandrills and their congener, drills (*Mandrillus leucophaeus*), were traditionally considered to be forest baboons, they are more closely related to *Cercocebus mangabeys* than they are to *Papio* species (Disotell, 1996; Fleagle and McGraw, 1999).

Male mandrills possess a suite of exaggerated visual, olfactory and acoustic traits. They have a bright red stripe down the nose, accentuated by blue paranasal ridges, a red penis, a lilac scrotum, and a multi-colored rump that includes red, blue, violet and lilac skin (Osman Hill, 1970; Setchell and Dixson, 2001a). Female mandrills also show bright red and blue skin color on their faces, the expression of which varies greatly across individuals (Setchell et al., 2006b), and pink anogenital skin. Like females of many other Old World primate species, female mandrills have exaggerated sexual swellings around the time of ovulation (Dixson, 2012).

In addition to their extraordinary coloration, mandrills also show pronounced sexual size dimorphism: adult male mass is 3.4 times that of females, making them the most sexually dimorphic primate and one of the most sexually dimorphic mammals (Setchell et al., 2001). Adult males also possess formidable weapons, with upper canines that can be up to 5 cm in height (Leigh et al., 2008), longer than any other primate (based on data in Plavcan and van Schaik, 1992).

Mandrills are extremely difficult to study in the wild, due to their dense forest habitat and very large home ranges (Harrison, 1988). Studies of wild mandrills have therefore concentrated on feeding ecology, group counts, and ranging behaviour (Hoshino et al., 1984; Hoshino, 1985; Lahm, 1986; Harrison, 1988; Rogers et al., 1996; Abernethy et al., 2002; White et al., 2010). These studies have shown that mandrills are omnivorous, eating fruit, seeds, leaves, pith, flowers, invertebrates and vertebrates (Rogers et al., 1996; Tutin et al., 1997) and use a very large home range unevenly (total area of 182 km² over a 6 year period, including 89km² of suitable forest habitat, but the mandrills spent more than half the time in <10% of this area: White et al., 2010). While groups of fewer than 50 are reported (Rogers et al., 1996), films of wild mandrills crossing forest gaps or roads yield group sizes of 338-845

at Lopé National Park (Rogers et al., 1996; Abernethy et al., 2002) and 169-442 in Moukalaba-Doudou National Park (Hongo, 2014), both in Gabon. These studies also reveal a low secondary sex ratio in comparison with other African papionins (Hongo, 2014; but see Rogers et al. 1996), and that males are also found solitary (Harrison, 1988; Rogers et al., 1996; Hongo, 2014). Group counts suggest that there are no adult males in the group at some times of year in the very large groups inhabiting Lopé National Park, and that male presence in the group increases with the number of females with sexual swellings present (Abernethy et al., 2002). Group counts of large groups at Moukalaba-Doudou National Park always include at least some adult males (Hongo, 2014). Finally, a group of mandrills originating from CIRMF and released into a private park within the species' natural range (Lékédi Park, Peignot et al., 2008) provide a habituated group living in the wild. A group of 120 travel 0.44-6.50 km/day in a home range of 866.7 ha, with permanent presence of males in the group (Brockmeyer et al., 2015).

The CIRMF mandrills

Due to the difficulty in following individual wild mandrills long-term, much of our understanding of mandrill behavioral and evolutionary ecology derives from studies of a colony housed at the Centre International de Recherches Médicales de Franceville, Gabon (CIRMF). The CIRMF mandrill colony is by far the largest population of captive mandrills in the world. The mandrills live in naturally rain-forested enclosures within their natural habitat range. The enclosures are large enough for solitary males to be able to avoid contact with the social group (Wickings and Dixson, 1992a). The colony was founded in 1983/4, when CIRMF released 7 males (estimated ages 2–4 years) and 8 females (estimated ages 1–6 years) into Enclosure 1 (6 ha) (Feistner et al., 1992) and left them to breed naturally. In 1994 several matriline groups were moved from Enclosure 1 into Enclosure 2 (3.5 ha), establishing a second semi-free-ranging group. From 1983 to 2006, when data collection for the studies reviewed here ceased, 307 animals were born into the colony, belonging to five maternal generations. Over time, 100 animals were removed, three escaped and 59 died. Group sizes ranged from the original 15 to a maximum of 104 in Enclosure 1 in 2002, corresponding to smaller groups observed in the wild (Rogers et al., 1996).

The CIRMF enclosures include fenced, concrete pens for provisioning and capturing the animals. Seasonal fruit and vegetables and monkey chow are supplied twice daily. As for the rhesus macaques (*Macaca mulatta*) of Cayo Santiago (Maestripietri and Georgiev, 2015), this provisioning can be seen as analogous to a clump of large fruiting trees, which produce

large crops daily. Water is freely available from a stream running through both enclosures and from water dispensers. Veterinary interventions are limited to badly wounded animals and to annual physical examinations. All mandrills are tattooed on the chest or inner thigh with an identification number. Animals over the age of 2 years are also given ear-tags to aid identification. Infants are usually caught and tattooed when they are still carried by their mother. When this system fails, the identity of unidentified juveniles is established via genotyping.

The naturalistic environment of the CIRMF colony, long-term daily observations of known individuals, the opportunity to capture animals periodically to collect morphological data and biological samples, and the availability of historical records and banked DNA and serum samples for most individuals have provided a unique opportunity to study individual animals long-term. However, disadvantages associated with colony conditions include the influence of provisioning on behaviour and life history, the influence of veterinary intervention on health, condition and survival in the case of injury, limited dispersal and predation, and a lack of gene flow and inbreeding (Charpentier et al., 2006).

Mandrill societies

Early studies in the wild suggested that mandrills lived in multi-level societies, similar to those found in hamadryas baboons (*Papio hamadryas*) and geladas (*Theropithecus gelada*), with large multi-male, multi-female groups composed of smaller one-male, multi-female units (Hoshino et al., 1984). However, observations at CIRMF showed that this was not the case, at least under colony conditions. Instead there is always one dominant male associated with the social group of females and their offspring, while other males vary in the extent to which they associate with the group (Wickings and Dixson, 1992b; Setchell and Dixson, 2001a). There is no evidence for male-female associations that resemble one-male, multi-female units, or that the multi-male, multi-female group splits into sub-groups with one male in each at CIRMF. Data for wild mandrills support this conclusion, as groups of varying sizes include no, one or several males (Hoshino et al., 1984; Abernethy et al., 2002), and studies of progression also suggest that mandrills do not live in multi-level societies (Hongo, 2014).

Mandrills mate moderately seasonally at CIRMF (Setchell and Wickings, 2004a), with 63 % of peri-ovulatory periods occurring between July and September, and only 6 % between December and April (Setchell and Wickings, 2004a) and a corresponding birth peak in January to March (Setchell et al., 2002). Data for wild mandrills show a similar pattern:

females with sexual swellings are usually observed from June to November at Lopé National Park (Abernethy et al., 2002).

LIFE HISTORY, THE ONTOGENY OF SEX DIFFERENCES AND MATERNAL EFFECTS

Animals have finite resources to allocate to growth, maintenance and reproduction. Life history theory suggests that these allocation decisions, and the schedule and duration of key events across an individual's lifetime, are shaped by natural selection to maximise fitness (Stearns, 1992). A developmental and long-term perspective is, therefore, fundamental to studies of sexual selection (Pereira and Leigh, 2003; Setchell and Lee, 2004). In this section, I address sex differences in mandrill behaviour, reproductive careers and growth and ontogeny, then discuss maternal effects on offspring growth and development.

Sex differences in behaviour

Mandrills are a classic example of conventional mammalian sex roles. Females show prolonged investment in infants, including the energetic demands of lactation and gestation common to all mammals and prolonged physical and social care for offspring, as in other primates (van Noordwijk, 2012). In contrast, male parental care is very limited, although affiliation between juveniles and males is higher among father–offspring dyads than among unrelated dyads (Charpentier et al., 2007), males protect their offspring from perceived threats (Laidre and Yorzinski, 2008), and in one case the top-ranking male in a CIRMF group often carried his infant son when the mother died (E. J. Wickings pers comm). These sex differences in reproductive priorities lead to large differences in how the two sexes behave.

Like many other Cercopithecine monkeys (Cords, 2012), female mandrills inherit their mother's dominance rank, with the youngest daughter ranking just below the mother (Setchell et al., 2008a). Female ranks in the CIRMF colony are linear and transitive, with all members of one matriline in a cluster, and have changed very little, beyond births and deaths, since they were first recorded in the 1980s. Female rank corresponds to the order in which the founder females arrived at CIRMF with the exception of those that have been removed from the enclosures and replaced much later who are at the bottom of the hierarchy (Setchell, unpublished data).

Males up to age 5 years are permanently associated with their social group, but peripheralize as they mature, spending time on the edge of their group or solitary (Setchell and Dixon, 2002; Setchell et al., 2006c). Group counts in the wild imply that adolescent

males are also under-represented in social groups (Abernethy et al., 2002), suggesting that they disperse, as in many other Cercopithecine species (Cords, 2012). Wild males have also immigrated into a group of mandrills released into a private park in Gabon (Brockmeyer et al., 2015), supporting this interpretation. In one case a male at CIRMF dispersed by jumping from one enclosure to another (Setchell et al., 2006c), but otherwise males either remain solitary or rejoin the group when they are full size (Setchell and Dixson, 2002; Setchell et al., 2006c). Top-ranking males are usually found in the centre of the social group, and are the most highly group-associated males (Setchell et al., 2006c). Males that gain alpha rank increase in the percentage of days they spend in the centre of the social group, while those who lose rank usually decrease, although less markedly (Setchell and Dixson, 2001b). As in the wild (Abernethy et al., 2002), more males are associated with the social group when receptive females are available (Setchell, unpublished data).

Sex differences in reproductive careers

In sexually dimorphic, polygynous species, like mandrills, life history theory predicts sex differences in age-specific reproductive output and mortality profiles, and greater variance in lifetime reproductive success in males than in females (Clutton-Brock, 1988). Tests of these predictions remain relatively rare, particularly for polygynandrous and long-lived species, due to the lack of long-term demographic and genetic data to address them. Short-term studies covering one or a few mating seasons can artificially inflate estimates of male reproductive skew, as male rank changes over the course of adolescence and adulthood.

We examined age-specific reproductive output and mortality in the CIRMF mandrills (Table 1). Female mandrills begin to reproduce at a mean age of 4.3 years and produce one infant at a time at a mean interval of 405 days (Setchell et al., 2002, 2005a). The distribution of inter-birth intervals is bimodal, with peaks at 1 and 2 years (Setchell, unpublished data), in accordance with moderate reproductive seasonality. Female reproductive output is relatively constant from 5 to 22 years, at which point it decreases. In contrast, the mean age at first reproduction for males is 11.6 years, by which time females already have several offspring (Setchell et al., 2005a). Mean male reproductive output is lower than for females until 10 years, peaks at 12 years, and decreases again to 0 by 19 years. Average lifespan in males is two-thirds of that in females (14 vs. >22 years) (Setchell et al., 2005a). The oldest males cease to reproduce, and some males experience a long post-reproductive period (Leigh et al., 2008). Variance in reproductive output is far greater in males than in females. While all female mandrills of breeding age in the CIRMF colony have produced offspring, only one in

three males sire (Setchell et al., 2005a). However, the reproductive output of a successful male is far more offspring than a female can bear in a lifetime (maximum 41 offspring in males, 17 for females, Setchell et al., 2005a). The influence of the colony conditions, including provisioning, lack of predation and a lack of dispersal opportunities, on these patterns remains unclear (details in Setchell et al., 2005a).

Male and female reproductive careers in mandrills thus conform to the predictions of sexual selection theory (Setchell et al., 2005a). These findings contribute to a relatively small set of long-term studies of genetically determined reproductive success in large mammals (Clutton-Brock, 1988; Coltman et al., 1999; Kruuk et al., 1999; Altmann and Alberts, 2003; Dubuc et al., 2014b). They suggest that the degree of polygyny, and therefore the strength of sexual selection in males, is extremely high, as in other highly sexually dimorphic animals (Coltman et al., 1999; Tatarenkov et al., 2008; Vanpé et al., 2008). Variance in male reproductive success is higher than in rhesus macaques, the only other anthropoid species for which data on lifetime reproductive success are yet available (Dubuc et al., 2014b). In addition to the implications for selection on males, the proportion of females and males contributing to the gene pool of a social group has implications for patterns of relatedness, and the opportunity for kin selection (Altmann, 1979, 1996; Charpentier et al., 2007; Widdig, 2013; Dubuc et al., 2014b).

Sex differences in growth and ontogeny

Intense competition between males for mating opportunities suggests selection for large male body size, and thus sexual dimorphism, as females are not selected to grow as large as males are. Adult sexual dimorphism can develop via sex differences in either growth rates or the duration of growth, or via a combination of the two (Shea, 1986; Leigh, 1992). Among anthropoid primates, sex differences in growth rate tend to occur in species living in social groups with one adult male and multiple adult females, while sex differences in the duration of growth (bimaturism) occurs in species with multiple adults of both sexes (Leigh, 1995).

Male mandrills are born slightly larger than females, but the majority of their adult mass dimorphism is achieved after weaning through a combination of sex differences in length of the growth period (females attain adult body mass at 7 years, males at 10 years) and growth rate (Wickings and Dixson, 1992a; Setchell et al., 2001). Although both males and females undergo puberty and can reproduce by about 4 years (Setchell et al., 2005a), males continue to grow for a further 6 years resulting in a much larger body size (Setchell et al., 2001). Male secondary sexual traits began to develop at the age of six years, shortly after the

testes began to increase in size, and one year before testosterone levels begin to increase markedly. Statural growth ceases at 9-10 years, while mass peaks at 10-12 years, and declines markedly in males aged 18 years and older. Male canines erupt at 5-9 years and are longest in males aged 9-11 years, after which canine height diminishes through breakage and wear (Leigh et al., 2008). Some old males have very small, blunt canines. The testes descend at a mean of 3.8 years but remain small until 5.5 years. Testicular volume then increases to a maximum at around 13 years, later than the peak in body mass (Setchell et al., 2006c). Secondary sexual trait expression is highly variable in both adolescents and adult males (Wickings and Dixson, 1992b; Setchell and Dixson, 2001a; b, 2002).

Maternal effects on offspring growth and development

Maternal traits affect offspring fitness in many species, via influences on offspring growth, development and physiology (Bernardo, 1996; Mousseau and Fox, 1998). Such maternal programming may arise from the mother's social environment, nutrition, reproductive experience and age, as well as via age-related changes in maternal condition and reproductive strategy (Stearns, 1992).

We tested for maternal effects in mandrills, finding that maternal age and rank are related to somatic growth in both sexes. Higher-ranking female mandrills have heavier infants than lower-ranking females and older female mandrills also have heavier infants than younger mothers (Setchell et al., 2001). These early advantages persist after weaning, when mothers are no longer investing directly in offspring (Setchell et al., 2001). Sons of higher-ranking mothers mature faster and are more likely to survive to adulthood than those of low-ranking mothers (Setchell and Dixson, 2002; Setchell et al., 2006c). Sons of heavier mothers also mature faster (Setchell et al., 2006c). Among females, dominance rank is inherited from mother to daughter (Setchell et al., 2008a), and dominant females have their first infant on average 1.3 years earlier than lower ranking females (Setchell et al., 2002), resulting in a large reproductive advantage to the daughters of dominant females.

Thus, mandrills show pervasive maternal effects, as do baboons (*Papio* spp. Johnson, 2003; Altmann and Alberts, 2005; Gesquiere et al., 2005; Charpentier et al., 2008; Onyango et al., 2008). However, the mechanisms by which these effects are mediated are not well understood. To shed light on this question, we examined potential maternal effects on three components of the endocrine regulation of growth (insulin-like growth factor-I, growth hormone binding protein and free testosterone) in infant, juvenile and adolescent mandrills (Bernstein et al., 2012). We described age-related patterns of these bioactive factors, and

found that maternal rank and parity influenced variation in concentration of all three bioactive factors in males. This suggests that these factors may provide important mechanistic pathways through which mandrill mothers modify the developmental trajectory, and thus the fitness, of their offspring (Bernstein et al., 2012).

MALE-MALE COMPETITION

The evolutionary consequences of male-male competition have been a focus of attention since the early days of primate behavior and ecology (Zuckerman, 1932; Carpenter, 1942; Altmann, 1962), and remain so today (Alberts, 2012). The nature of competition between males is determined by whether they can monopolize females, which is, in turn, determined by the spatiotemporal distribution of receptive females (Emlen and Oring, 1977; Shuster and Wade, 2003). Where females are clumped in space and time, theory predicts that male reproductive output will be skewed towards dominant males. Here, I address the implications of the mandrill's polygynandrous mating system, in which receptive females are clumped in space (social groups) and in time (the mating season) for male-male competition, including physical aggression and dominance rank, the relationship between male rank and reproductive success, alternative reproductive tactics, post-insemination sperm competition, the social modulation of testosterone, social stress, weaponry, whether red color acts as a badge of status (Rohwer, 1975, 1977; Rohwer and Rohwer, 1978), and chemical signalling.

Physical aggression and dominance rank

As predicted on the basis of their very large size and impressive weaponry, male mandrills compete physically. The rate of male injury increases from age 5 years, when young males experience only minor injuries at a rate of just 5% of males per year, to peak at 11–12 years, when, on average, half of all males experience serious injury in a given year, and 75% experience minor injuries. The majority of injuries occur in months when sexually receptive females are available (Setchell et al., 2006c), suggesting that they result from contests over access to these females.

Top rank is highly contested among male mandrills, and take-overs of the top position usually involve death or serious injury to the incumbent (Setchell et al., 2006c). Male dominance rank increases with age from 6 to 11 years, peaks at 11-16 years, then decreases, producing an inverted U-shaped curve of rank vs. age (Setchell et al., 2006c). This is likely to reflect age-related changes in competitive ability, matches age-related reproductive success (Section 4.2), and is similar to other primate species where males compete for access to

receptive females (van Noordwijk and van Schaik, 1985, 1988). The pattern of dominance rank in the CIRMF mandrills has a less pronounced peak than observed in wild savannah baboons (*Papio cynocephalus*: Packer et al., 2000; Alberts et al., 2003), perhaps due to the lack of immigrating males and low mortality among older males at CIRMF (Setchell et al., 2006c).

Tenure as top-ranking male has a mean of 25 months (range 1-96 months, n=7) in the CIRMF colony. Removing one outlier reduces the mean to 13 months. Tenure is related to group demography, and decreases with increasing numbers of rival adult males and maturing adolescent males (Setchell et al., 2006c). The mean is considerably longer than the average tenure in savannah baboons (8 months, Alberts et al., 2003) or chacma baboons (*Papio ursinus*, 5 months, Palombit et al., 1997), again possibly because of the closed conditions of the CIRMF colony (Setchell et al., 2006c).

Reproductive advantages of top rank

The relationship between male dominance rank and reproductive success varies both across and within primate species (van Noordwijk and van Schaik, 2004). In multi-male, multi-female societies where males compete for dominance rank and access to receptive females, the priority-of-access model predicts that where receptive females are asynchronous, the top-ranking male will monopolise reproduction, but where more than one female is receptive simultaneously males of lower ranks will also obtain mating opportunities, according to the number of females available and the male's rank (Altmann, 1962; Hausfater, 1975).

Early studies at CIRMF showed that top-ranking males sired 80-100% of offspring in any one mating season (Dixson et al., 1993). Subsequent, extensive paternity studies confirmed this high reproductive skew in favour of top-ranking males, who sired 76% of offspring from 1983 to 2002 (Charpentier et al., 2005). Dominant male mandrills mate-guard receptive females, following them persistently and attempting to prevent other males from gaining access to them (Setchell et al., 2006c). Combining behavioural data on mate-guarding with paternity analyses for 1996 to 2002, we showed that both periovulatory mate-guarding and paternity outcome correlated significantly with male rank (Setchell et al., 2005b). Alpha males accounted for 94% of periovulatory mate guarding and 69% of paternity (a result slightly different from Charpentier et al. 2005 as the data do not span the same period). Mate-guarding is therefore a good predictor of paternity, but overestimates the reproductive success of the top-ranking male, showing that females mate polyandrously (Setchell et al., 2005b). The observed distributions of both mate-guarding and paternity fit the priority-of-access

model well. However, top-ranking males accounted for a greater proportion of both mate-guarding and reproduction than predicted by the model (Setchell et al., 2005b). We do not know how these findings reflect the situation in the wild, but wild males may have more opportunity to employ alternative tactics in the wild, than at CIRMF, potentially lowering monopoly by the top-ranking male.

The emerging picture from the growing number of studies that have addressed the predictions of the priority-of-access model in primates is that, in general, it is accurate, but that deviations from the model differ between species. As in mandrills, top-ranking male chimpanzees (*Pan troglodytes*) sire more offspring than expected from the model in some studies (Boesch et al., 2006; Newton-Fisher et al., 2010), but sire fewer offspring than expected in other studies (Wroblewski et al., 2009). Among other species top-ranking males sire fewer offspring than expected (savannah baboons: Alberts et al., 2006; rhesus macaques: Dubuc et al., 2011; Assamese macaques, *Macaca assamensis*: Sukmak et al., 2014). It is, as yet, unclear whether these differences result from methodological differences or actual differences in male strategy (Sukmak et al., 2014), or from the interaction of male and female strategies.

Alternative tactics

As the number of adult males increases, the proportion of mate-guarding by top-ranking male mandrills decreases (Setchell et al., 2005b). Mate-guarding also becomes less effective, and translates into fewer paternities, as the number of reproductive males increases. These patterns can be attributed to the employment of alternative reproductive tactics by subordinate males, including furtive copulations (Setchell et al., 2005b). As in other polygynandrous primates (savannah baboons: Alberts et al., 2003; rhesus macaques: Widdig et al., 2004), these results for mandrills support limited or incomplete control models of reproductive skew, which predict that subordinates will reproduce when the capacity of dominant individuals to monopolize reproduction is reduced (Cant, 1998; Clutton-Brock, 1998; Reeve et al., 1998).

Monopolisation of females by high-ranking males can lead to the evolution of other alternative reproductive tactics in male primates. These include coalitions that force a male to relinquish a female and forming “friendships” with particular females (reviews in: Setchell and Kappeler, 2003; Setchell, 2008; Alberts, 2012). We have not studied these in detail, but there is no evidence of obvious coalitions against mate-guarding males, or of particular affiliative relationships between unrelated males and females.

Alternative tactics may also include delayed development in subordinate males (Setchell and Kappeler, 2003; Setchell, 2008; Dixson, 2012). Studies of the six founder males in the CIRMF colony found that they fell clearly into two groups as adults. “Fatted” males were social, brightly colored, with large testes and a stocky appearance, while “nonfatted” males were paler, with smaller testes and less developed secondary sexual traits (Wickings and Dixson, 1992a). This suggested that subordinate, “nonfatted” males may be physiologically suppressed by intense intra-sexual competition, in a similar fashion to unflanged male orang-utans (*Pongo* spp., Maggioncalda et al., 1999; Utami et al., 2002). Arrested development of secondary sexual characteristics may allow competitively inferior males to avoid both aggression and the costs of high levels of testosterone (Setchell, 2003). However, subsequent study revealed that male mandrills fall on a continuous spectrum of possibilities between highly developed, highly group-associated males, and solitary males with muted secondary sexual characteristics (Setchell and Dixson, 2001a). This suggests that adult male mandrills represent a more complex phenomenon than the two distinct morphotypes originally proposed.

Post-insemination sperm competition

Species with a polygynandrous mating system are predicted to have adaptations for sperm competition. For example, they have larger testes for body weight than species that are polygynous or monogamous, reflecting relative opportunities for sperm competition and the benefits of producing and ejaculating a large number of sperm where females mate with multiple males (Short, 1979; Dixson, 2012). Mandrills have relatively large testes for their body size (Dixson, 2012). Variation in testes size among males is very large and in adolescent males this variation correlates with the development of other sexual traits, as well as with their dominance rank (Setchell et al., 2006c). Among the founder males of the CIRMF colony, dominant males had larger testes than subordinate males (Wickings and Dixson, 1992b), but later work found that top-ranking males do not necessarily have the largest testes (Setchell et al., 2006c). Adult males also experience changes in testes size: new top-ranking males show an increase in testes size, while deposed top-ranking males show a decrease in testes size (Setchell and Dixson, 2001b). These findings are in line with the mandrill’s polygynandrous mating system and suggest a high degree of sperm competition (Dixson, 2012). Intra-specific variation in testes size related to social and reproductive status also occurs in other primate species (review in Dixson, 2012).

Mandrill testes increase in size during the mating season, by an average of 25% (Setchell and Dixson, 2001c). This is less than in rhesus macaques, where the testes increase in volume by 50–70% (Sade, 1964; Wickings and Nieschlag, 1980), and far less than in the highly seasonal lemurs, such as Coquerel's giant mouse lemur (*Mirza coquereli*), where testes size increases 5-fold during the mating season (Kappeler, 1997).

Like other species with a high degree of post-insemination competition, mandrills show sperm coagulation after copulation, with a visible deposit in the female's vagina (Dixson, 2012). Such plugs may promote sperm survival and maintain sperm-rich ejaculate in close contact with the os cervix to encourage sperm transport in the female reproductive tract (Dixson, 2012). Males of polygynandrous species should also produce high volume, sperm-rich, high quality ejaculates, to aid in sperm competition. For example, in some bird species, male phenotype correlates with sperm traits (Kempnaers et al., 1992), whereas in others, socially subordinate males have superior sperm (Froman et al., 2002). However, collecting naturally-produced ejaculate is challenging, and as yet, we know nothing about sperm production, ejaculate volume or quality in mandrills and how this might relate to pre-copulatory strategies. This is in line with a general paucity of the mechanisms of sperm competition in primates, mainly because it is difficult to achieve the experimental control needed to study them, although mouse lemurs provide an exception (Birkhead and Kappeler, 2004).

Social modulation of testosterone

The steroid hormone testosterone influences male sexual behaviour, aggression, displays and secondary sexual characters in vertebrates (Dixson, 2012). Where males compete for high rank, as in mandrills, dominant males might be expected to have higher levels of testosterone. However, high levels of testosterone are costly (Wingfield et al., 1997). For example, in addition to promoting costly behaviours, testosterone may compromise immune function, and increase both stress levels and the risk of mortality (Marler and Moore, 1988; Folstad et al., 1996; Braude et al., 1999). This balance of cost and benefit underpins the "challenge hypothesis", which holds that testosterone promotes aggression when it is beneficial to males, for example during the development of dominance relationships or when males challenge one another for access to mates (Wingfield et al 1990).

Testosterone measured in plasma samples obtained at captures suggested that testosterone increases with dominance rank in male mandrills (Wickings and Dixson, 1992b; Setchell and Dixson, 2001a). We extended this by using non-invasive fecal androgen analyses

to test the relationships between testosterone and behaviour (Setchell et al., 2008b). We found that fecal androgens in male mandrills are positively related to dominance rank, suggesting that males live in a permanently aggressive context in which they must actively maintain their dominance status (Setchell et al., 2008b). Androgens also increase when male ranks are unstable and when receptive females are available, both situations in which males compete intensely (Setchell et al., 2008b). These results support the challenge hypothesis, and reflect patterns found in many other taxa (Oliveira, 2004; Hirschenhauser and Oliveira, 2006), including other male primates living in multi-male, multi-female societies with high potential for male-male competition (Muller and Wrangham, 2004; Beehner et al., 2006; Higham et al., 2013a).

Social stress in males

Social interactions, including those associated with dominance rank, can be important sources of stress. The vertebrate stress response includes activation of the hypothalamus–pituitary–adrenal axis and the release of glucocorticoids into the bloodstream. Glucocorticoids mobilize energy and divert it from physiological processes that are not required for immediate survival, such as digestion, growth, immunity and reproduction (Sapolsky, 2000, 2002). While this is adaptive in the short-term, chronic elevation of glucocorticoids has deleterious effects that include reproductive failure and compromised disease resistance. We found that the relationship between fecal glucocorticoids and rank depends on the stability of the dominance hierarchy in male mandrills (Setchell et al., 2010a). When the dominance hierarchy is stable cortisol levels are higher in lower ranking males, supporting the “stress of subordination” hypothesis. However, when the hierarchy is unstable, this relationship is reversed, supporting the “stress of dominance” hypothesis. These patterns are likely to be due to differences in the predictability of the social environment during stable and unstable periods. We also found an interaction between dominance rank and the presence of receptive females: dominant males had higher glucocorticoids than subordinate males, but only when receptive females were available, reflecting the costs of competition for females. These findings for mandrills reflect patterns in other polygynandrous primates, where the relationship between glucocorticoids and dominance rank also depends on the social environment (e.g., Sapolsky, 1992, 1993; Bergman et al., 2005; Ostner et al., 2008; Higham et al., 2013a; Cheney et al., 2015).

Male weaponry

The fitness consequences of changes in armaments across life are poorly understood, limiting our understanding of the evolution of weaponry. We used long-term data on male canine height, rank and reproductive success to test the hypothesis that canine tooth eruption, adult canine size and tooth wear correlate with male fitness in male mandrills (Leigh et al., 2008). We found that canine height is strongly correlated with male reproductive success, suggesting sexual selection for canine size. Canine height matches the curve of reproduction vs. age very closely and sires have longer teeth than males that do not reproduce (Leigh et al., 2008). These results are the first to demonstrate close ties between fitness and armaments in male primates and further illustrate the need to incorporate life history into studies of sexual selection (Section 4). Moreover, canines are exceptional, in that they are non-renewable, unlike other kinds of mammalian weaponry, such as horns, antlers, and body mass, which can be renewed either continually or periodically.

Male color as a badge of status

Red color on the face, genitalia and rump is brighter in top-ranking male mandrills than in other males (Wickings and Dixson, 1992b; Setchell and Dixson, 2001a; b; Setchell et al., 2008b). Higher-ranking males also display more saturated blue, and thus a stronger contrast between the two colors, than lower-ranking males (Renoult et al., 2011). The dramatic red color is related to testosterone, suggesting that male red is a dynamic signal of competitive ability and willingness to fight (Wickings and Dixson, 1992b; Setchell and Dixson, 2001a; b; Setchell et al., 2008b). Males gaining top rank increase in red color and testosterone (Setchell and Dixson, 2001b). Red coloration develops after a male has attained top rank (Setchell et al., 2008b) and the extent of red coloration increases with tenure as dominant male, providing additional potential information concerning competitive ability. Dominant males that lose their top rank decrease in both testosterone and color (Setchell et al., 2008b). Post-dominant males may retain dots of red in their blue paranasal ridges, providing a potential signal of the traits that allowed them to hold top rank (Setchell et al., 2008b), perhaps via permanent changes in gene expression and skin receptor populations.

Similar relationships with male rank have been reported for red color on the lower lip and groin in male drills (Marty et al., 2009) and on the chest in male gelada (Bergman et al., 2009) but not for facial red in male rhesus macaques, a difference that may be linked to weaker male-male competition in this species (Higham et al., 2013b; Dubuc et al., 2014a). These findings suggest that red color may act as a badge of status, informing rivals as to the competitive ability of the bearer and allowing the assessment of rivals without escalated

combat (Rohwer and Ewald, 1981; Andersson, 1994; Bradbury and Vehrencamp, 1998). We tested this hypothesis in mandrills by examining the relationship between color and male behaviour (Setchell and Wickings, 2005). We found that unidirectional submission occurs where males are very different in color, while threats, contact aggression and unresolved “standoff” encounters are more common between males that are similar in color. These results suggest that male mandrills use the relative brightness of their red coloration to facilitate the assessment of individual differences in fighting ability, regulating the degree of costly, escalated conflict between well-armed males (Setchell and Wickings, 2005). However, experiments are needed to determine whether color alone determines male interactions, in the absence of other cues, including social knowledge of the individual male. For example, differences in scrotal blue color predicted dominance rank when unfamiliar male vervets (*Chlorocebus pygerythrus*) were introduced to one another (Gerald, 2001). Experimental manipulations of scrotal blue color did not support this finding, but did show that more aggression occurred between males that were similar in color than between those that were different in color, supporting the hypothesis that male color mediates social interactions (Gerald, 2001).

Chemical signalling in males

The chemical composition of mammalian olfactory signals can reflect species, sex, group and individual identity, as well as current social, reproductive and health status (Wyatt, 2003; Thom and Hurst, 2004; Brennan and Kendrick, 2006). However, chemical communication has been neglected in comparison with other sensory modalities in primates, particularly in catarrhines (Heymann, 2006). Nevertheless, there is increasing evidence that olfaction plays an important role in primate social behaviour (Drea, 2015). Mandrills possess a sternal gland (Hill 1970), which produces a glandular secretion which they rub vigorously against tree trunks and branches (Feistner, 1991). They also possess nasopalatine ducts (Osman Hill, 1970; Charpentier et al., 2013) and some animals show a flehmen-like behaviour in response to conspecific odorants, suggesting that odor plays a role in communication (Charpentier et al., 2013). Males scent-mark more than females, and top-ranking males mark more than subordinates (Feistner, 1991). Scent-glands are also maximally active in top-ranking males (Setchell and Dixson, 2001a; b).

We used gas chromatography-mass spectrometry to investigate the volatile components of mandrill scent-gland secretion collected during captures and to compare odor profiles with features of the signaller (Setchell et al., 2010b, 2011b). We found that odor

profiles differed by sex, but the odor profiles of younger males resembled those of females. We could also differentiate between adolescent and adult males and between top-ranking and subordinate males, and between samples collected during mating periods and non-mating periods. These relationships reflect those described in strepsirrhines and platyrrhines (review in Drea, 2015), supporting a role of odor in reproductive signalling, and suggest that odor may reflect testosterone levels, although we have not tested this relationship directly. In the deep forest environment, where males are not permanently associated with the social group (Abernethy et al., 2002), scent-marks may provide an important signal of the presence and status of a rival male. Unlike visual and auditory signals, odor continues to inform conspecifics in the absence of the signaller (Gosling and Roberts, 2001), although we do not yet know how long such signals persist in mandrills.

FEMALE CHOICE

Female choice was relatively ignored for more than a century after Darwin proposed it. However, since the 1970s it has become the subject of extensive theoretical and empirical attention (Andersson, 1994). Many questions remain open, including the mechanisms underlying the evolution of mate choice, the costs of choice, the genetic correlation between traits and preferences, the situations under which mutual mate choice evolves, the evolution of multiple traits, and the relative contributions of the various models of mate choice within and between taxa (Jones and Ratterman, 2009), making this an exciting field.

Three major models of mate choice differ in what the choosy sex obtains (Andersson, 1994). First, choosers may select mates because they provide the greatest direct benefits to the chooser, including resources or parental care. Second, choosers may receive no immediate, measurable benefits, but instead obtain indirect, genetic, benefits. These include genes that influence the attractiveness of offspring to the opposite sex (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982), or some aspect of viability, such as heritable “quality” (Zahavi, 1975), developmental stability (Møller and Swaddle, 1997) or pathogen resistance (Hamilton and Zuk, 1982; Folstad and Karter, 1992; von Schantz et al., 1996), often reflected in exaggerated traits. Third, choosers may obtain no benefits at all, if mate choice favors traits which exploit pre-existing sensory biases (Ryan and Keddy-Hector, 1992) or which are exaggerated in order to overcome the chooser’s resistance (Holland and Rice, 1998). Mate choice can be both direct, where choosers discriminate between the attributes of potential mates, and indirect, which describes any other behavior which restricts the chances of mating with particular

individuals (Wiley and Poston, 1996). It can be expressed pre- and post-copulation, or via differential allocation of resources to particular mates (Burley, 1986; Sheldon, 2000).

A 2004 review noted “surprisingly little evidence for female choice in primates” and that it is “woefully understudied” (Kappeler and van Schaik, 2004b, p9, p12). However, we have examined female mate choice in mandrills in three ways: via testing for biases in pre-copulatory behaviour in favour of particular male traits, by comparing the genotype of actual sires with all potential sires at the level of the individual offspring, and by testing for post-copulatory selection.

Pre-copulatory female choice for male rank and color

Although male mandrills are much larger than females, and males mate-guard females, females can still decide which males to mate with because their smaller size allows them to escape up trees. I have never witnessed overt sexual coercion in the form of attacks or harassment of females by males, unlike reports in chimpanzees, for example (Muller et al., 2011). Female mandrills exhibit proceptive choice by sexually soliciting some males more than others, and receptive choice by refusing unwanted mating attempts by avoiding the male's approach or by lying down when a male attempts to copulate (Setchell, 2005). Observations of these behaviours show that female mandrills express mate choice for both top-ranking males and for more colorful males (Setchell, 2005). The correlation between female choice behaviour and male color is stronger than that between female choice and male rank, and partial correlations between female behavior and male color are stronger than between female behaviour and male rank, suggesting that male coloration has an influence separate from, and more important than, that of male rank.

Female choice for high-ranking males in mandrills reflects similar findings in other primate species (e.g., brown capuchins *Cebus apella*: Janson, 1984; Welker et al., 1990; vervet monkeys: Keddy, 1986; long-tailed macaques, *Macaca fascicularis*: de Ruiter and van Hooff, 1993; Barbary macaques, *Macaca sylvanus*: Paul et al., 1993; drills: Marty et al., 2009) and may indicate choice for direct benefits, in the form of protection for the female herself or of the resulting offspring, or indirect benefits, in the form of genes for quality that lead to the acquisition of high rank.

Unlike female mandrills, female drills do not show choice for male color, once the effect of rank is accounted for (Marty et al. 2009). However, experiments show that female brown lemurs (*Eulemur fulvus*) and rhesus macaques look at images of more brightly colored males for longer than they do females of less brightly coloured males (Cooper & Hosey 2003;

Waitt et al. 2003). While attention does not necessarily indicate sexual attraction, female rhesus macaques also make more sexual solicitations to images of dark red males than to images of pale pink males, suggesting that they are attracted to the darker males (Dubuc et al., 2014a).

Testing good genes models

“Good genes” models of sexual selection state that sexual traits serve as reliable indicators of the bearer’s genetic quality. For example, the “handicap” hypothesis predicts that only individuals of superior quality will be able to express costly ornamentation (Zahavi, 1975; Grafen, 1990; Andersson, 1994), although the mechanisms maintaining the honesty of such signals are the topic of ongoing debate (Lachmann et al., 2001; Grose, 2011; Számadó, 2011). The parasite-mediated sexual selection hypothesis, an extension of the handicap hypothesis, suggests that ornaments reliably reflect an individual’s ability to resist parasites by revealing current health status (Hamilton & Zuk 1982; Moller & Saino 1994). The immunocompetence handicap hypothesis (Figure 1), extends this model further, positing that testosterone-dependent ornaments signal the ability to cope with the immunosuppressive effects of testosterone (Folstad & Karter 1992). Under these models, members of the opposite sex should choose the most ornamented mate because these high quality mates provide fitness benefits, either directly, through avoidance of parasite transmission and increased investment in offspring or both, or indirectly, by passing on good genes for vigor and health to offspring (Able 1996; Andersson 1994; Hamilton & Zuk 1982; Zahavi 1975). The major histocompatibility complex (MHC) is an excellent candidate for such good genes, due to the critical role it plays in the immune system, encoding cell-surface glycoproteins that recognize foreign peptides, presenting them to specialist immune cells and initiating the appropriate immune response (Klein 1986).

The mandrill is the only primate species in which the relationships shown in Figure 1 have yet been examined in detail. We have already seen that red color is related to rank and testosterone (Section 5.8; Fig 1, arrow A). We also found that red is related to the possession of specific MHC genotypes (Fig 1, arrow F), suggesting that only individuals of superior genetic quality may be able to express color fully, and providing some support for the hypothesis that ornaments advertise good genes (Setchell et al., 2009). However, it remains to be seen whether these particular MHC genotypes are beneficial in terms of parasite resistance (Fig 1, arrow C) or fitness. We found no evidence that red is related to parasitism, immune status or genetic diversity in individual males (Fig 1, arrows B, F), limiting the support for the

parasite-mediated sexual selection hypothesis for the evolution of color in male mandrills (Setchell et al., 2009). However, the provisioned nature of the study population may obscure relationships between signals and condition, if all the animals are healthy.

An alternative formulation of the immunocompetence handicap hypothesis, the stress-mediated hypothesis for the evolution of condition-dependent traits, suggests that the handicap functions via a trade-off between glucocorticoid levels and the immune system (Møller, 1995; Siva-Jothy, 1995; Hillgarth and Wingfield, 1997; Westneat and Birkhead, 1998; Braude et al., 1999). If subordinate males suffer elevated glucocorticoid levels, this may suppress their immune system, and prevent them from producing testosterone and, therefore, red color. We conducted the first test of this hypothesis in mammals (Setchell et al., 2010a). The relationship between glucocorticoids and male rank depends on the stability of the dominance hierarchy (Section 5.3, Fig 1, arrow A). However, although male mandrills with higher glucocorticoid levels harbored a higher diversity of parasite infection (Fig 1, arrow E), we found no significant relationship between glucocorticoids and red color (Fig 1, arrow A), providing little support for the stress-mediated hypothesis for the evolution of sexual signals in mandrills (Setchell et al., 2010a).

MHC-associated mate choice

MHC-associated mate choice is hypothesized to provide offspring with a fitness advantage through disease resistance in three non-mutually exclusive ways. First, choice for particular beneficial genotypes may provide offspring with resistance to particular parasites (Penn and Potts, 1999). This choice for good genes yields an additive fitness benefit. Second, choice for an optimal diversity of MHC genes in the offspring may lead to enhanced pathogen resistance (Doherty and Zinkernagel, 1975; Penn and Potts, 1999; Reusch et al., 2001) or more generally to increased genetic diversity in offspring (Brown and Eklund, 1994). This choice for MHC-dissimilarity was originally thought to involve choice for maximum diversity, but the negative consequences of excessive differences may lead to choice for an optimal intermediate level of MHC diversity in offspring (Wegner et al., 2003; Woelfing et al., 2009). Third, choice for an MHC-diverse mate may maximise offspring heterozygosity regardless of the chooser's own genotype (Reusch et al., 2001), or pass on rare, beneficial, alleles to offspring (Apanius et al., 1997).

We genotyped as many of the CIRMF mandrills as possible for MHC-DRB and compared the genotype of the sire of each offspring with the genotype of all potential sires using a multinomial discrete choice model (Setchell et al. 2010b). Surprisingly, given the

strong influence of male dominance rank on male reproductive success, we found that genetic factors also influence male reproductive success. The probability of siring increases with MHC dissimilarity to the mother, and with male MHC diversity, suggesting selection for both genetic compatibility and genetic diversity (Setchell et al. 2010b). We found no influence of the possession of individual specific genotypes on siring. These results were the first to demonstrate mate choice for genetic dissimilarity in a species with high male reproductive skew, and suggest that MHC-associated mate choice can occur even where male–male competition is intense. While the closed nature of the CIRMF colony may increase the need for mate choice to avoid closely related individuals, it cannot explain the ability to do so. Together with a handful of studies of other primate species, these results suggest that MHC-associated mate choice is widespread across the primates and occurs in diverse social and mating systems (Setchell and Huchard, 2010).

Odor may provide a way in which mandrills can assess genotype in their conspecifics, and a possible mechanism underlying MHC-associated mate choice for both genetic diversity (good genes) and genetic dissimilarity. When we compared our odor profile data with MHC genotypes, we found that odor profile diversity reflected MHC diversity in males, while dyadic odour similarity was strongly related to MHC similarity (Setchell et al., 2011b). This evidence of “odortypes” (Yamazaki et al., 1994) in mandrills also suggest that odor may underlie mandrills’ ability to discriminate paternal kin (Charpentier et al., 2007). However, we could not discriminate reliably between individuals possessing particular MHC genotypes based on odor profiles (Setchell et al., 2011b), in contrast to our findings for red color, which is linked to particular genotypes (Setchell et al., 2009).

These findings for mandrills are the first to show a link between MHC genotype and odor in a non-model species, but odor also correlates with genome-wide diversity and genetic relatedness in ring-tailed lemurs (*Lemur catta*, Charpentier et al., 2008a, 2010; Boulet et al., 2010), suggesting that these patterns may be widespread in the primate order. Future studies should examine the relationship between odor profile and parasite burden, and test whether mandrills, or other primates, can discriminate between parasitized and non-parasitized individuals, as rodents can (e.g., Kavaliers and Colwell, 1995; Willis and Poulin, 2000).

Cryptic female choice

We know little about post-copulatory mate choice in primates (Birkhead and Kappeler, 2004). It is very difficult to study post-copulatory mate choice under naturalistic conditions, as it requires information on exactly who a female mates with and when, throughout her fertile

period. However, this difficulty can be circumvented, to some extent, by concentrating on selection between the sperm of one male: the sire (Setchell et al., 2013). We can be sure that the sperm of the sire were present in the female's reproductive tract at the appropriate time, and can use the haploid nature of sperm to test for selection within a male. We tested for post-copulatory selection mechanisms for MHC haplotypes in mandrills, by comparing the MHC haplotypes of the parental dyad with those of the offspring to test whether post-copulatory sexual selection favoured offspring with two different MHC haplotypes, more diverse gamete combinations, or greater within-haplotype diversity (Setchell et al., 2013). We also tested for any influence of materno-fetal compatibility (Ober, 1999) on MHC-haplotype inheritance. Our sample size of 127 offspring and parents allowed us only to test for medium or large effect sizes. Within these limitations, we found no evidence of post-copulatory female choice for male genotype in mandrills (Setchell et al., 2013). This contrasts with evidence for MHC-associated post-copulatory selection in mouse lemurs (*Microcebus murinus*, Schwensow et al., 2008), the only other non-human primate in which this has been investigated.

FEMALE-FEMALE COMPETITION

If we broaden our view of sexual selection to include the sources of variation in female fitness (Clutton-Brock, 2007, 2009; Carranza, 2009; Gowaty and Hubbell, 2009), then this includes female-female competition for the resources required for pregnancy and lactation as well as for access to desired mates (Clutton-Brock, 2007, 2009; Stockley and Bro-Jørgensen, 2011). We have investigated female-female competition in mandrills in terms of the reproductive benefits of high social status, androgens, social stress, the possibility that female color signals female rank or testosterone, and chemical signalling.

Reproductive benefits of high social status

In general, dominance rank is associated with fitness in female primates (meta-analysis in Majolo et al., 2012). This is also true for the CIRMF mandrills. In addition to the effects of rank on offspring growth, development and fitness (Section 4.4), higher-ranking females experience their first sexual cycles on average 6 months earlier than lower-ranking females, giving birth for the first time at a younger age and showing shorter inter-birth intervals (Setchell and Wickings, 2004a; Setchell et al., 2005a). These findings reflect a general pattern of shorter inter-birth intervals in high-ranking than in low-ranking female primates (Pusey, 2012). In mandrills, there is no rank-related difference in the time taken to resume cycling after birth, and the difference in inter-birth intervals is reflected in higher-ranking females

requiring fewer cycles to conception than lower-ranking females (Setchell and Wickings, 2004a). This contrasts with results for Amboseli baboons, where shorter inter-birth intervals in high-ranking females appear to be due to shorter post-partum amenorrhea rather than to improved probability of conception in a given cycle (Beehner et al., 2006b). As yet, we have no information on whether the ovulatory nature of cycles varies with female rank in mandrills.

Provisioning is likely to accelerate maturation and reproductive rates in the CIRMF mandrills, compared to wild mandrills (Lee and Bowman, 1995), although as yet there are no data for wild mandrills to confirm this. Abundant resources may equalise variance in female reproductive success (Fedigan et al., 1986), but may also accentuate it, if high-ranking females enjoy greater feeding success on clumped resources. There is no relationship between female rank and body size in the CIRMF mandrills, however (Setchell, 1999).

There appears to be no simple effect of female-female competition for access to males on whether female mandrills conceive, as the number of receptive females available does not influence the probability of conception (Setchell and Wickings, 2004a) unlike in geladas (Dunbar and Sharman, 1983) and captive hamadryas baboons (Zinner et al., 1994). Whether female mandrills compete for access to particular males is less clear, although there are theoretical reasons to predict that they should, if female choice converges on the same male and female cycles coincide. Female baboons target follicular phase females for aggression (Wasser and Starling, 1988; Huchard and Cowlshaw, 2011), but this does not appear to be competition for sperm, as the attackers themselves are not always cycling (Stockley and Campbell, 2013). Asynchrony of cycles could promote fertilisation by the most desired male, if there is competition for particular mates (Pereira, 1991; Matsumoto-Oda and Hamai, 2007). However, although female mandrills show a seasonal peak in cycling from July to September, female cycles in our long-term records (10 group-years) are no more nor less synchronised than a chance distribution (Setchell et al., 2011a). Despite the popular appeal of the concept of menstrual synchrony, these results are in line with critical reviews showing that synchrony has not yet been demonstrated convincingly (e.g., Schank, 2001).

Finally, we found little effect of female rank on offspring survival in mandrills (Setchell et al., 2002), in contrast to the results of a meta-analysis for primates in general (Majolo et al., 2012). This difference may relate to the very low levels of offspring mortality in the CIRMF colony low, which 90% of infants survive to 6 months (Setchell et al., 2002).

Female androgens and dominance rank

Androgens are typically regarded as male hormones, and their biological significance in female primates has received less attention than in males. We examined fecal androgens in female mandrills, and found no relationship between androgens and rank (Setchell et al., 2015). This contrasts strongly with our results for males (Section 5.2), reflecting sex differences in competitive behaviour. Our results for female mandrills reflect patterns found in females of some other primate species (savannah baboons: Altmann et al., 1995; ring-tailed lemurs: von Engelhardt et al., 2000; bonobos, *Pan paniscus*: Sannen et al., 2004), but not others, in which higher-ranking females show higher androgen levels than lower-ranking females (talapoin, *Miopithecus talapoin*: Batty et al., 1986; hybrid baboons, *Papio hamadryas hamadryas* x *P. h. anubis*: Beehner et al., 2005; Barbary macaques: Grant et al., 2011). As yet, we lack a comprehensive understanding of the link between rank and androgens in female primates, but these species differences may relate to how rank is attained, and maintained (Setchell et al., 2015).

Social stress in females

Subordinate female primates often show greater glucocorticoid production than dominant females, supporting the “stress of subordination” hypothesis (review: Cavigelli and Caruso, 2015). We hypothesised that the reduced reproductive success we observed in low-ranking females relative to high-ranking females might be related to chronic stress in the former. If this was the case, we expected to find higher fecal glucocorticoid levels in low-ranking females than in high-ranking females, and that high fecal glucocorticoid levels would be linked to reduced fertility. However, we found no support for these predictions (Setchell et al., 2008a). This contrasts with our results for males (Section 5.3), and suggests that subordinate female mandrills are able to avoid dominant animals, use alternative foraging strategies, and / or buffer social stress through social relationships (Abbott et al., 2003). It may also relate to the inheritance of female rank, as the stress of subordination hypothesis is more strongly supported in primate species where rank is not inherited than in those where rank is inherited (review: Cavigelli and Caruso, 2015).

Female facial color and female-female competition

Female secondary sexual traits have received far less attention from evolutionary biologists than those of males (Andersson, 1994), although primate sexual swellings are a notable exception to this rule (Clutton-Brock, 2007). Female traits have traditionally been considered as non-adaptive by-products of selection for the same trait in males (Darwin, 1871; Lande,

1980; Kraaijeveld et al., 2007). However, phylogenetic analysis of birds suggests that genetic constraints are not strong (Price and Birch, 1996), suggesting that we should seek adaptive explanations for female traits (Amundsen, 2000; Clutton-Brock, 2007, 2009).

Facial color varies greatly between individual female mandrills, from an entirely black face to a bright pink mid-nasal stripe with blue paranasal ridges similar to that of a subordinate adult male (Setchell et al., 2006b). Color also varies within females, although less than across females. In contrast to our findings for males (Section 5.7), facial red is unrelated to rank in females, suggesting that it does not function in resource competition (Setchell et al., 2006b).

Few studies have tested the relationship between female ornamentation and natural variation in androgen levels, but studies in birds have shown that testosterone is positively correlated with female color (Jawor et al., 2004; Muck and Goymann, 2011; Moreno et al., 2014). We tested this relationship in mandrills, finding an overall positive relationship between mean facial color and mean fecal androgens in females (Setchell et al., 2015), reflecting the pattern we found in males (Setchell et al., 2008a). However, the relationship was negative when we accounted for female identity (Setchell et al., 2015). Further studies are thus required to clarify the relationship between female color and testosterone.

Chemical signalling in females

Female mandrills scent-mark less than males, although dominant females mark more than subordinates (Feistner, 1991). In contrast to our findings for males, we found no relationship between odor profile and rank in female mandrills (Setchell et al., 2010b).

MALE CHOICE

In general, male mate choice has been subject to far less attention than mate choice by females, and the same is true for primates (Alberts, 2012; Kappeler, 2012). However, a modern definition of mate choice holds that it occurs whenever traits expressed in one sex lead to a bias in the allocation of mating and reproductive investment by the other (Halliday, 1983; Kokko et al., 2003). As in females, males should apportion costly reproductive effort in relation to the quality of a mate to maximise their reproductive success. Male choice has been shown in many animals, including insects, fish, lizards, fish, birds, and mammals (Bonduriansky, 2009; Clutton-Brock, 2009).

Reproduction is costly for male mandrills, in terms of time and energy invested, as well as the risk of aggression from rival males and injury. Top-ranking males lose mass over

mating season, suggesting that mate-guarding is costly (Setchell and Dixson, 2001c), as in other primate species with high male-male competition (e.g., savannah baboons: Alberts et al., 1996; Japanese macaques, *Macaca fuscata*: Matsubara, 2003; long-tailed macaques: Girard-Buttoz et al., 2014b). Sexual selection theory predicts, therefore, that males should show mate choice for higher quality females. We investigated this in terms of choice according to likelihood of conception within a cycle, direct benefits and female genotype, as well as in relation to female secondary sexual traits (sexual swellings and facial color) and odor.

Allocation of male effort within a cycle

The best evidence for mate choice in male primates comes from studies showing that males concentrate mating effort when a female is most likely to conceive, both within a female cycle (review: Setchell and Kappeler, 2003; chimpanzees: Deschner et al., 2004; Thompson and Wrangham, 2008; long-tailed macaques: Engelhardt et al., 2004; Barbary macaques: Heistermann et al., 2007; baboons: Gesquiere et al., 2007; Higham et al., 2009), and by preferentially mating with conceptive females rather than those that do not conceive (Bulger, 1993; Weingrill et al., 2000, 2003; Alberts et al., 2006; Gesquiere et al., 2007). In line with this, male mandrills preferentially mate-guard on days when females are most likely to be fertile and mate-guard conceptive cycles in preference to non-conceptive cycles (Setchell et al., 2005b).

Male choice for direct benefits

Female mandrills vary in the direct benefits they can provide to offspring. For example, multiparous and higher-ranking females are more likely to conceive than nulliparous and lower-ranking females, and produce larger offspring when they do so (see Section 4.4). As predicted by sexual selection theory, males show mate choice by preferentially mate-guarding higher-ranking and multiparous females relative to lower-ranking and nulliparous females (Setchell and Wickings, 2006). Similar choice for high-ranking females occurs in macaques, baboons and vervets (early studies reviewed in Berenstein and Wade, 1983; vervets: Keddy-Hector, 1992; long-tailed macaques: de Ruiter et al., 1994; Girard-Buttoz et al., 2014a; Barbary macaques: Kuester and Paul, 1996), and males also prefer older or parous females in other species (earlier studies reviewed in Anderson, 1986; chimpanzees: Muller et al., 2006; ring-tailed lemurs; Parga, 2006; long-tailed macaques: Girard-Buttoz et al., 2014a).

Male choice for female genotype

Few studies to date have addressed the question of male choice for indirect benefits, which enhance the genetic quality of the offspring. Male pipefish (*Syngnathus typhle*), a species with extreme paternal care, choose females that maximise MHC diversity in offspring (Roth et al., 2014), but studies of other fish report no relationship between male mate choice and female MHC genotype (Forsberg et al., 2007; Neff et al., 2008; Bahr et al., 2012). Male red junglefowl (*Gallus gallus*) show no overt mate choice, but allocate more sperm to the more MHC-different female in pair-choice experiments (Gillingham et al., 2009).

We developed a statistical model based on 10 years of observations to describe how the probability a female mandrill is mate-guarded varies across her sexual cycle, among cycles and among females and combined this with MHC genotyping to test for MHC-associated mate choice in males (Setchell et al in review). We found that mate-guarding was related to particular female MHC genotypes and was highest in pairs with intermediate MHC differences. Male mate-guarding was not, however, linked with female MHC diversity. We also found that the MHC genotype that attracted the least mate-guarding was disadvantageous in terms of parasite abundance and immune function, suggesting a fitness benefit to male mate choice. These findings are the first to link natural precopulatory mate choice behaviour in males to female MHC genotype in a non-model organism with conventional sex roles. They show that highly competitive males can also show mate choice, a behaviour traditionally assigned to females, and suggest that choice for MHC genotype extends much further than currently thought. A question for the future is whether and how female behavior influences male mate-guarding behavior.

Sexual swellings

Sexual swellings are hypothesised to act as reliable indicators (*sensu* Hamilton and Zuk, 1982) of female reproductive success. This hypothesis predicts that swelling characteristics, such as size and color, correlate with aspects of female mate quality, and that males should base their mating decisions on these traits, preferring to mate with those with more exaggerated characteristics (Pagel, 1994). Swelling size in mandrills varies more between females than within females across swelling cycles, implying that swelling size is a relatively consistent characteristic of individual females (Setchell and Wickings, 2004b; Setchell et al., 2006a). However, we found little evidence that differences in sexual swelling size and color between female mandrills reliably advertise female quality (Setchell and Wickings, 2004b; Setchell et al., 2006a). Specifically, females with higher reproductive success do not show

larger or brighter sexual swellings (Setchell and Wickings, 2004b). Swelling color is negatively related to body mass index and age, and unrelated to rank or parity (Setchell and Wickings, 2004b). Moreover, swelling size is not significantly related to measures of parasitism and immune status, nor to genetic diversity (Setchell et al., 2006a). There is also little evidence that male mandrills allocate more mating effort to females with particular swelling characteristics (Setchell and Wickings, 2004b). Male mate-guarding is not significantly related to female swelling characteristics. Females with wider sexual swellings are more likely to have a copulatory plug when maximally swollen, but there is no relationship between the presence of copulatory plugs and other swelling characteristics (length, depth or color). Furthermore, in situations in which more than one female was maximally swollen, the alpha male (who has “free” choice) did not show the most interest in the female with the largest swelling.

This lack of support for the "reliable indicator" hypothesis in mandrills is in line with evidence from other primate species. Although one highly cited study of baboons supported the hypothesis (Domb and Pagel, 2001), reanalysis of the data cast doubt on the conclusions (Zinner et al., 2002) and careful analysis of the results of subsequent tests of the predictions of the reliable indicator hypothesis suggests that primate sexual swellings do not signal differences in fitness across individual females (Fitzpatrick et al., 2015).

The “graded signal” hypothesis, which holds that exaggerated swellings convey the probability of ovulation within a cycle, has received more support in studies of various primate species (e.g., chimpanzees: Deschner et al., 2004; Barbary macaques: Brauch et al., 2007; baboons: Gesquiere et al., 2007; Higham et al., 2008, crested macaques, *Macaca nigra*: Higham et al., 2012), although this is not the case in all species (e.g., long-tailed macaques: Engelhardt et al., 2005; Assamese macaques: Fürtbauer et al., 2011). We have not yet tested this hypothesis in mandrills.

Finally, swelling size varies by up to 10% between cycles within individual mandrills (Setchell et al., 2006a). Such variation may indicate swelling cycle-to-cycle variability in the probability that an individual female conceives (Zinner et al., 2002; Emery and Whitten, 2003), but there is no significant difference in swelling size between conceptive and non-conceptive cycles in mandrills (Setchell et al., 2006a). Endocrine data are needed to test whether swelling size provides reliable information about the quality of a particular cycle in mandrills, as in other species (e.g., chimpanzees: Emery and Whitten, 2003; Deschner et al., 2004; savannah baboons: Gesquiere et al., 2007).

Female facial color and “quality”

We tested the hypothesis that female facial color signals reproductive quality and that only high quality individuals can maximally express such traits (Zahavi 1975; Hamilton & Zuk 1982). We found no evidence that facial color is related to female reproductive quality, measured as the age at first birth or the mean inter-birth interval, or to body condition, measured as body mass index or the residual of a regression of body size to skeletal size (Setchell et al., 2006b). Nor is female color related to parasitism, immune parameters or genetic diversity, although it is related to the possession of specific MHC genotypes, as in males, although the specific genotypes differ between the sexes (Setchell et al., 2009). Female color may signal one aspect of reproductive quality, as younger and nulliparous females are both darker-faced than older and parous females, and of lower mate quality as they are less fertile (Setchell and Wickings, 2004a) and produce smaller offspring (Setchell et al., 2001). However, some older females can also be very dark-faced, casting some doubt on this interpretation.

Female mandrills are brighter-faced during the follicular phase than during the luteal phase of their menstrual cycle (Setchell et al., 2006b). This suggests that female facial color may advertise fertility and sexual receptivity, perhaps by acting as a graded signal of fertility (Nunn, 1999b). Similar findings have been reported for red facial color in female rhesus macaques (Dubuc et al., 2009), although not for anogenital color in rhesus macaques (Dubuc et al., 2009) or baboons (Higham et al., 2008).

Female color also varies across gestation in mandrills and peaks 4-8 weeks post-parturition (Setchell et al. 2006b) at which point females are an extremely bright pink. These changes do not have an obvious fit to changes in hormones across the female reproductive cycle in primates, although we have not yet measured female hormones in mandrills. We proposed a possible adaptive explanation for this finding: that a peak in coloration signalling the presence of a ventral infant, which is vulnerable to infanticide, may attract care from candidate sires (van Schaik and Janson, 2000; Buchan et al., 2003). Infanticide has occurred when new males were added to the CIRMF colony (CIRMF unpublished records).

Chemical signalling and female quality

We found no relationship between odor profile and genetic diversity or specific genotypes in female mandrills (Setchell et al., 2010b). We were unable to differentiate between cycling, lactating, pregnant and quiescent females based on sternal gland secretion (Setchell et al., 2010b), but we did not address changes across the menstrual cycle, due to limited sample

size. However, males clearly attend to female genital odor, sniffing females' genitalia closely (Setchell, 1999), suggesting that they may discriminate cycle stage based on odor, as in several other primate species (review in Drea, 2015).

SUMMARY AND SYNTHESIS, WILD MANDRILLS AND WHY MANDRILLS ARE SO EXTREME

The semi-free-ranging mandrill colony at CIRMF has allowed us to conduct a range of studies, combining analyses of social behavior, demography, morphology, endocrinology, pathogens, genetics, and chemistry to investigate questions about a fascinating and unusual primate. These studies have revealed a great deal about sexual selection in both sexes, with some occasionally surprising findings. Here, I summarise and synthesise these results, comparing the two sexes, discuss the need to study wild mandrills, and explore why mandrills are so extremely sexually dimorphic.

Summary and synthesis

We have shown how different reproductive priorities lead to very different life histories and divergent adaptations in males and females. A long-term approach has revealed pervasive effects of maternal rank and experience on offspring growth and fitness, and we have begun to unravel the potential physiological mechanisms underlying this.

Intra-sexual competition leads to physical aggression in males and achieving top rank brings great reproductive advantages, in line with the priority-of-access model. This leads to alternative tactics in subordinate males, and males also compete post-insemination via sperm competition. Competition between females may be less conspicuous than that in males, but there is substantial variation between females in offspring quantity and quality, and clear reproductive benefits of high social status. We found little support for the popular idea that female menstrual cycles are synchronized, which would promote female-female competition, nor for asynchrony of cycles within the mating peak, which would alleviate such competition.

Testosterone increases with dominance rank in males, and is higher when male ranks are unstable and when receptive females are available, supporting the challenge hypothesis. In contrast, female androgens are not linked to rank, which is stable. In males, glucocorticoids are higher in lower-ranking males when the hierarchy is stable, but higher in higher-ranking males when it is not. In females we found no relationship between rank and glucocorticoids, suggesting that differences in social stress do not underlie the observed rank-related differences in female reproductive success. These sex differences in the relationship between

glucocorticoids and rank are likely to be due to differences in the predictability of the social environment in the two sexes.

Both sexes of mandrill show mate choice, for both similar and different traits (Table 2). Both sexes choose for high rank in the opposite sex, which may indicate choice for direct or indirect benefits. Both sexes also choose for indirect benefits in the form of complementary genes, although there is more support for males selecting for intermediate differences than the maximum differences females prefer. In addition, males also choose for reproductive experience (direct benefits) and specific MHC genotypes (indirect benefits) in females, but not for genetic diversity. Males do not choose based on between-individual differences in sexual swelling size or color, but we do not yet know whether they choose for female facial color. Males show mate choice within a cycle based on the likelihood of conception, but not based on between-individual differences in sexual swellings. In addition to rank, females choose for male color and genetic diversity (indirect benefits), but not for specific genotypes. These results show that females of a highly sexually dimorphic species with high reproductive skew towards top-ranking males can still express mate choice, via biases in pre-copulatory behaviour and, possibly, post-copulatory selection. Moreover, mandrills provide some of the first evidence that males choose females based on the indirect benefits of female MHC genotype.

Overall our results concerning secondary sexual traits provide clear evidence of sexual selection for male secondary sexual traits, but less so for females (Table 3). Male secondary sexual traits are closely linked to intra-sexual selection (dominance rank), but this is not the case for females. We have found evidence of female choice in favour of particular male (red color), but not female, phenotypic traits. Male canine height is related to reproductive success, and, although we have not tested the relationship between other male traits and reproductive success directly, color and odor are both related to dominance rank, which is strongly related to reproductive success. In contrast, female secondary sexual traits are not linked to reproductive success.

Male red color acts as a badge of status and signals current androgen status, but is not related to glucocorticoids. In contrast to male color, female color appears to have a complex relationship with testosterone. We have not yet tested the relationship between female color and glucocorticoids. Tests of good genes models for the evolution of sexual traits link color to specific MHC genotypes in both sexes, although not to parasitism, immune status or genetic diversity (Table 3). This provides little support for parasite-mediated sexual selection hypotheses for the evolution of these traits, although the colony conditions may reduce

variation in health among the CIRMF mandrills, masking any such relationship. Male odor is linked to genetic diversity in males, although the evidence is partial, but not in females. Odor is not linked to specific MHC genotypes in either sex. Importantly, odor provides a potential mechanism by which mandrills may detect their optimal mate in terms of good genes and complementary genes and mandrills provide the first evidence for MHC odortypes in a non-model organism.

Finally, we have not yet tested the graded signal hypothesis (Nunn, 1999b) for the evolution of sexual swellings in female mandrills, but female facial color increases around the fertile period and may signal ovulation. For the moment, however, we cannot exclude the possibility that female color represents a genetically correlated response to selection on males (Lande, 1980) and that there are no adaptive explanations for variation in female color. In support of this hypothesis, differences in color within females are smaller than those that occur between females, and females never attain the brilliant red of an alpha male. If this is the case, then female color represents a baseline of expression in the absence of consistent and strong selection, and can inform us as to the relationship between color and hormones.

Comparisons with wild mandrills

The CIRMF colony provides a very useful compromise between the benefits of accessibility and long-term information on individual animals and the disadvantages of captivity and provisioning. Although any patterns we find in captive animals represent adaptations that evolved in the wild, we should be cautious when generalising from this closed, provisioned population to wild mandrills. The presence of clumped, provisioned resources, a reduction in predation risk, and a lack of dispersal may all have implications for individual strategies. In addition to the potential influences of colony conditions noted elsewhere in this review, it seems likely that males at CIRMF have more social knowledge of one another and that females are more familiar with individual males than we can expect in the wild. There is a clear need to combine our understanding of reproductive strategies and signalling in semi-free-ranging animals with studies of wild mandrills.

Why are mandrills so extreme?

The overarching questions in much of this research concern why mandrills are quite so sexually dimorphic in body size, why males are so heavily armed and why they are so superbly ornamented, advertising with visual, olfactory and acoustic displays. The obvious answer to the evolution of very large body size and impressive weaponry is strong contest

competition over male dominance and high reproductive skew. However, this is also true of many less dimorphic primate species (Alberts, 2012). So what makes *Mandrillus* (mandrills and drills) so extreme? First, as noted in Section 4.2, comparative data on variation in male lifetime reproductive success are scant, but the CIRMF data (with their caveats) suggest that variance in male reproductive success may indeed be extreme in mandrills compared to other species (Setchell et al., 2005a). This arises from the combination of consistently high paternity concentration in the top-ranking male (this relationship is less predictable in other species, Alberts, 2012) and the number of reproductive females in a group. Second, *Mandrillus* species are the largest Old World monkeys, and larger species are also more sexually dimorphic than smaller species, so part of the explanation for the extreme sexual dimorphism may simply be overall body size (Plavcan and van Schaik, 1997). Third, sexual dimorphism may result from selection on females to be smaller, as well as on males to be larger, and we should not neglect the possibility that small size may be advantageous to females, due to increased investment in reproduction (Setchell and Lee, 2004). Fourth, *Mandrillus* species are classed as terrestrial. Substrate use influences sexual dimorphism in both body and canine size, with higher dimorphism in arboreal/terrestrial species than in arboreal species (including *Mandrillus*), although the greatest canine dimorphism values are in savannah-dwellers (Plavcan and van Schaik, 1992, 1997).

While canines function in male-male combat, large canines may also evolve to advertise fighting ability, allowing rivals to avoid dangerous escalation (Plavcan and van Schaik, 1992). Females may also attend to such armaments as signs of male quality, as they are not easily faked (Berglund and Pilastro, 1996). Male-male competition and female choice may also interact to explain exaggerated male ornaments. Studies of sexual selection tend to focus on either male-male competition or female choice, but the two mechanisms rarely operate independently (Hunt et al., 2009). A review of studies where both mechanisms act on the same male trait found that they act in concert in the majority of studies, either simultaneously or sequentially (Hunt et al. 2009). Most of these studies examined body size, but there are examples of male-male competition and female choice acting on the same color trait in male invertebrates, fish, reptiles, birds and mammals. Mandrills are the only mammals listed where both mechanisms act on the same ornamental trait (male color), but male mane color in lions (*Panthera leo*) provides a second example (West and Packer, 2002). It is not yet clear whether this relates to the rarity of the phenomenon or a lack of studies addressing the question.

Finally, it seems likely that extraordinary sexual dimorphism in mandrills is linked to their extraordinary group sizes (Abernethy et al., 2002), in which mating partners and rivals have limited social knowledge of one another (Setchell and Kappeler, 2003). Indeed, a recent comparative study showed that exaggerated male ornaments evolve in primate species with large, complex and more anonymous social organizations, like those of mandrills (Grueter et al., 2015).

FUTURE PERSPECTIVES

Beyond the need to study wild mandrills, our understanding of sexual selection in mandrills can be further improved in a variety of ways:

1. Studies of both male-male competition and female choice will be improved by the inclusion of post-copulatory mechanisms, to gain a full picture of influences on male reproductive success. However, such studies are challenging (Birkhead and Kappeler, 2004).
2. While male-male competition is well-studied, there are many future perspectives for the study of female-female competition (Clutton-Brock and Huchard, 2013; Stockley and Campbell, 2013). For example, detailed studies of female aggression will reveal exactly how females compete, for which resources, and how rank relates to the amount and quality of resources acquired.
3. We have shown that the MHC genotype which males prefer is linked to parasite abundance and immune function, and studies of lemurs also show that particular MHC genotypes are related to pathogen resistance (Schad et al., 2005; Schwensow et al., 2007), but we need further studies of the fitness consequences of mate choice.
4. We can improve measures of secondary sexual traits, including improved color measures that account for the mandrill visual system (e.g., Stevens et al., 2009).
5. We have not yet addressed the question of whether developmental asymmetry is linked to individual quality, reproductive success or sexual selection in mandrills, although the longitudinal furrows on the paranasal ridges are excellent candidate traits to highlight developmental symmetry. The usefulness of fluctuating asymmetry as a measure of developmental instability and associations with fitness remain unclear after 50 years of research (van Dongen, 2006). However, individual measures of condition are related to facial asymmetry in humans (meta-analysis in van Dongen and Gangestad, 2011), chimpanzees (Sefcek and King, 2007), and rhesus macaques (Little

et al., 2012), and symmetry is attractive in humans (Little et al., 2007), while rhesus macaques spend more time looking at images of symmetrical faces of the opposite sex than at asymmetrical faces (Waite and Little, 2006). Together, these results suggest that facial symmetry is also potentially important in sexual selection in mandrills.

6. We should employ improved measures of the potential costs associated with secondary sexual traits, although this can be challenging (Johnstone, 1995; Kotiaho, 2001; Számadó, 2011; Biernaskie et al., 2014). For example, although sexual swellings increase the body mass of females, divert fluids from other bodily functions and may attract blood-sucking insects (Nunn, 1999a), there are no detailed investigations of the costs of sexual swellings to female primates. Improved measures of immunocompetence (e.g., Drury, 2010) will improve tests of handicap hypotheses (Folstad and Karter, 1992). Oxidative stress has been proposed as a potential physiological mechanism linking ornament expression to genetic quality (von Schantz et al., 1999), prompting many studies in birds and fish (Garratt and Brooks, 2012). Recent studies suggest that oxidative stress markers can be used to measure the costs of reproductive effort in mandrills and rhesus macaques (Beaulieu et al., 2014; Georgiev et al., 2015). However, no studies have yet linked oxidative stress to ornaments in primates. Conspicuous color may also expose a male to increased predation risk, with dominant individuals being better able to escape, as in guppy fish (*Poecilia reticulata*, Endler, 1980).
7. Correlational studies provide weak tests of the relationship between secondary sexual traits and condition (Cotton et al., 2004). Ethical considerations preclude experimental manipulation of ornaments in a social context, but the administration of anti-parasite medication represents a possible approach to manipulating condition.
8. Mandrills signal in multiple sensory modalities: visual, auditory and olfactory. Such multiple traits may provide different information, or act as back-up signals (Candolin, 2003). For example, male mandrill color and odor both signal age and rank, but also reflect different male traits: red reflects testosterone and some MHC genotypes, while odor encodes genetic diversity and genetic similarity (Setchell et al., 2009, 2010b, 2011b). To date, we have not studied auditory signals, although males roar, and high-ranking adult males produce an energetic two-phase grunt. Similar calls appear to advertise competitive ability and dominance in baboons (Kitchen et al., 2003; Fischer et al., 2004). Future studies should examine the relative importance and signal content of these multi-modal and multicomponent signals.

9. Although both sexual swellings and facial color vary with the menstrual cycle, as yet we have no hormonal data to determine whether female secondary sexual traits relate to levels of reproductive hormones, or whether they convey information regarding female fertility and the timing of ovulation.
10. The studies of secondary sexual traits reviewed here have mainly focussed on the signal. We need studies of the receiver to determine whether mandrills of both sexes attend to variation in trait expression in both sexes, to determine the relative importance of various criteria, and to separate the roles of signals, social familiarity and behavior. For example, males may be more interested in the current state of a rival male, while females may be more interested in his underlying genetic quality, if females base mating decisions on genetic benefits that accrue to their offspring, rather than on direct benefits. We do not yet know whether female mammals choose males based on armaments, largely because it is difficult to disentangle choice from male-male competition (Clutton-Brock and McAuliffe, 2009). Presentation experiments can be conducted with visual traits (e.g., Cooper and Hosey, 2003; Waite et al., 2006; Dubuc et al., 2014a), odor (e.g., Charpentier et al., 2013; Drea et al., 2013) and auditory signals (e.g., Fischer et al., 2013). Both observational studies and experiments should incorporate endocrine measures to establish when females are fertile, as this may influence their mate choice.
11. A key aspect of indirect models of sexual selection is that sexually-selected traits should be heritable (Andersson, 1994). Studies in primates have only just begun to address this issue. A recent study of red skin color in rhesus macaques found that variation in red skin coloration is heritable (Dubuc et al., 2014c) and a preliminary study suggests that the same is true for mandrills (Setchell et al., unpublished data).

CONCLUSIONS

The studies reviewed here exemplify the potential of a long-term, multi-disciplinary approach that integrates field observations with laboratory methods to address important questions relating to sexual selection in primates. They also illustrate the potential of broadening our traditional perspectives on sexual selection beyond the ostentatious results of intense sexual selection on males in polygynous species to investigate more subtle and cryptic forms of competition and choice in both sexes. Expanding our investigation of intra-sexual competition to include competition over resources required for successful reproduction in both sexes and investigating mate choice in males as well as in females opens many productive avenues in

the study of primate reproductive strategies. Among other areas, these include the potential for studies of post-copulatory selection, female choice (which should no longer be woefully neglected), female intra-sexual competition, and male choice. Study of the two sexes allows us to investigate parallels between males and females, as well as fundamental differences in reproductive strategy, and the associated adaptations. Studies across groups, populations and species will allow us to investigate social and environmental influences on the action of sexual selection.

Primatology can contribute to important areas identified as requiring additional research in sexual selection, including the costs of choice, the genetic correlation between traits and preferences, the situations under which mutual mate choice evolves, the evolution of multiple sexually selected traits, and the relative contributions of the various models of mate choice within and between taxa (Jones and Ratterman, 2009). Comparative studies can take advantage of the wide variety of primate social and mating systems to illuminate why the intensity of sexual selection varies across populations and lineages. Primate studies rarely employ selection coefficients for sexually selected phenotypic traits (but see Lawler et al., 2005), or calculate Bateman gradients, a potential fruitful avenue for research on the factors affecting these (Jones and Ratterman, 2009). The long-term studies that characterise primatology (Kappeler and Watts, 2012) provide opportunities to employ a life history perspective and examine life-time fitness, while advances in the integration of field and laboratory studies will continue to open up new fields of discovery.

The study of sexual selection in mandrills has brought many insights into how and why the sexes differ in appearance and behaviour, and has the potential to yield far more. These findings and the future directions described in this review provide comparison and, I hope, inspiration for studies of other species, including both other polygynandrous species and species with mating systems less traditionally associated with sexual selection.

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Table 1: Comparative life history of male and female mandrills at CIRMF

	Females	Males
Rank	inherited	contested
Age first reproduction	4.3 +/- 0.3 yr	11.1 +/- 1.0 yr
Mean % lifespan spent pre-reproductive	22%	83%
Reproductive output	relatively constant from 5 to 22 yr; mean inter-birth interval 405 +/- ? d; low variation	lower than for females until 10 yr, peaks at 12 yr, and decreases again to 0 by 19 yr; high variation
Average lifespan	>22 yr	14 yr
Variance in reproductive output	all female mandrills of breeding age in the CIRMF colony have produced offspring	only one in three males in the CIRMF colony sire offspring
Maximum reproductive output	17 offspring	41 offspring
Attain adult mass	7 yr	10 yr
Age at puberty	4 yr	4 yr

Sources: Setchell et al., 2001, 2005

Table 2: Summary of mate choice criteria in male and female mandrills at CIRMF

Choosy sex	Chosen sex	Rank	Parity	Color	Sexual swellings	Likelihood of conception	Genetic diversity	Specific genotypes	Complementary genes
Males	Females	+	+	?	no	+	no	+	+ (quadratic relationship)
Females	Males	+	n/a	+	n/a	n/a	+	no	+ (linear relationship)

+ indicates a positive correlation, no indicates no evidence for a relationship, ? indicates an as-yet untested relationship

Sources: Setchell, 2005; Setchell and Wickings, 2006; Setchell et al., 2010; Setchell et al., in review

Table 3: Summary of relationships between secondary sexual traits, mechanisms of sexual selection, reproductive success and aspects of ‘good genes’ hypotheses in mandrills of both sexes

Sex	Trait	Relationship with (arrow in Fig 1 where relevant)							
		Intra-sexual competition (dominance rank)	Mate choice	Reproductive success	Androgens (A)	Glucocorticoids (A)	Genetic diversity (F)	Specific genotypes (F)	Pathogens and immune status (B)
Males	Canine height	+	?	+					
	Facial red	+	+	(+)	+	no	no	+	no
	Odor	+	?	(+)	?	?	+	no	?
Females	Sexual swellings	no	no	no	?	?	no	?	no
	Facial red	no	?	no	~	?	no	+	no
	Odor	no	?	?	?	?	no	no	?

+ indicates a positive correlation, no indicates no evidence for a relationship, ~ indicates a complex relationship, (?) indicates a relationship not yet tested explicitly, but which can be assumed because both variables correlate with rank, ? indicates an as-yet untested relationship, some cells are blank for canine height because it cannot respond once formed, although it may covary with aspects of phenotypic quality or relate to genotype. Numbers in () indicate the relevant section of the text

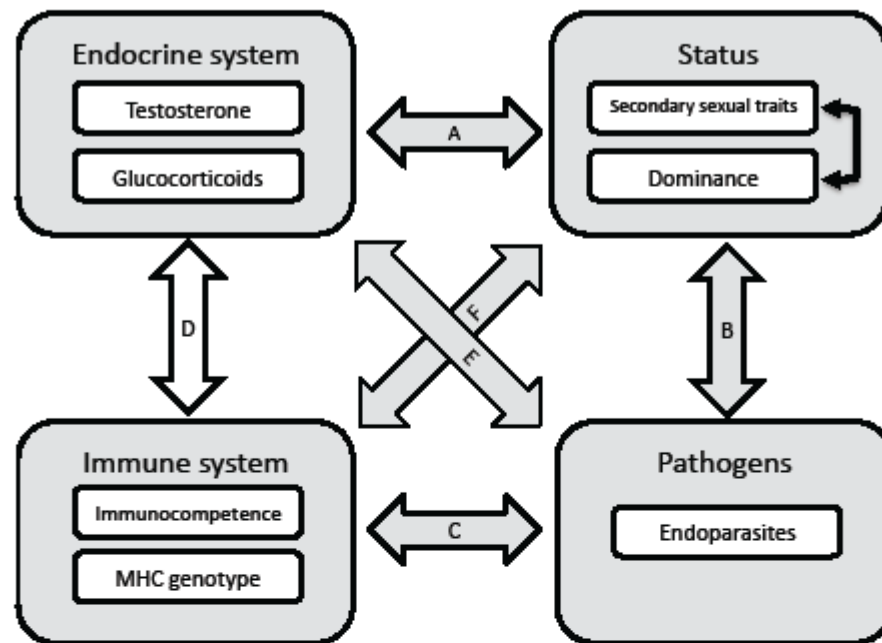


Figure 1: The immunocompetence handicap hypothesis, modified from Folstad & Karter (1992). Grey arrows show relationships tested in male mandrills. White arrows remain to be tested. Letters are referenced in the main text.