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Testosterone and reproductive effort in male primates

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Abstract

Considerable evidence suggests that the steroid hormone testosterone mediates major life-history trade-offs in vertebrates, promoting mating effort at the expense of parenting effort or survival. Observations from a range of wild primates support the “Challenge Hypothesis,” which posits that variation in male testosterone is more closely associated with aggressive mating competition than with reproductive physiology. In both seasonally and non-seasonally breeding species, males increase testosterone production primarily when competing for fecund females. In species where males compete to maintain long-term access to females, testosterone increases when males are threatened with losing access to females, rather than during mating periods. And when male status is linked to mating success, and dependent on aggression, high-ranking males normally maintain higher testosterone levels than subordinates, particularly when dominance hierarchies are unstable. Trade-offs between parenting effort and mating effort appear to be weak in most primates, because direct investment in the form of infant transport and provisioning is rare. Instead, infant protection is the primary form of paternal investment in the order. Testosterone does not inhibit this form of investment, which relies on male aggression. Testosterone has a wide range of effects in primates that plausibly function to support male competitive behavior. These include psychological effects related to dominance striving, analgesic effects, and effects on the development and maintenance of the armaments and adornments that males employ in mating competition.

Introduction

All organisms must manage fundamental trade-offs between growth, maintenance, and reproduction, in order to maximize fitness in changing environments. The endocrine system plays a key role in mediating life-history strategies, such as investment in current versus future reproduction, by coordinating morphological, physiological, and behavioral responses to environmental factors, including energy availability and social context (e.g. Ellison 2003, Stearns 1989, Wingfield et al. 2000, Zera & Harshman 2001). Substantial evidence suggests that the primary role of the steroid hormone testosterone is to promote reproductive effort, at the expense of long-term survival (Hau 2007; Ketterson & Nolan 1992, 1999). For example, testosterone drives the process of male genital development and supports sperm production

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(Dixson 2012, Weinbauer et al. 2004). It also spurs development of the secondary sexual characteristics that males use to compete with rivals and attract mates, including sexually dimorphic musculature (Bribiescas 2001, Kemnitz et al. 1988, Setchell et al. 2008). Finally, testosterone supports behavioral aspects of mating effort, by promoting both libido and aggression in reproductive contexts (Archer 2006, Dixson 2012, Isidori et al. 2005). Testosterone can adversely impact survival by increasing metabolic rate, exposure to predators, and risk of injury, and potentially by suppressing some aspects of immune function (Hilgarth & Wingfield 1997, Roberts et al. 2004, Wingfield et al. 2001).

Reproductive effort comprises both parenting effort, which is investment in offspring, and mating effort, which is investment in male-male competition and mate attraction. Elevated levels of testosterone predictably increase mating effort in vertebrates, and actively suppress parental activities in many species (Ketterson & Nolan 1999). Trade-offs between mating and parenting effort are widespread, as time and energy expended on male-male competition cannot normally be invested in offspring (Magrath & Komdeur 2003, Trivers 1972). As we shall see, however, not all forms of parenting are incompatible with mating effort (Stiver & Alonzo 2009). Silverback gorillas, for example, protect their offspring from infanticidal males, a form of paternal care that simultaneously functions as mating effort, since females abandon males who are ineffective defenders (Watts 1989). Testosterone is not expected to interfere with this type of investment.

The importance of testosterone in facilitating reproductive aggression is emphasized by the “challenge hypothesis,” which was originally formulated to explain both interspecific and individual differences in testosterone production by seasonally breeding birds (Wingfield et al. 1990). At the individual level, circulating testosterone in birds increases slightly during the breeding season, supporting spermatogenesis, sexual interest, and courtship behaviors. Following this initial rise, testosterone levels show transient surges to much higher concentrations during periods of social instability and heightened male aggression - “especially when establishing a territory, when being challenged by another male, or when mate guarding” (Wingfield et al. 2006:192). Under stable social conditions, and particularly when males are engaging in paternal care, testosterone levels are reduced back to baseline. Data from more than 80 bird species are consistent with these predictions (Hirschenhauser et al. 2003, Wingfield et al. 2000). Experimental manipulations in a range of birds have confirmed that high levels of testosterone often suppress parental behavior (De Ridder et al. 2000, Hegner & Wingfield 1987, Peters et al. 2002, Schoech et al. 1998, Stoehr & Hill 2000, Van Roo 2004), though not always (Lynn et al. 2002, 2005; Van Duyse et al. 2000).

At the species level, the challenge hypothesis predicts that the magnitude of the testosterone response to social instability is determined by mating system (specifically the form of male reproductive competition) and breeding strategy (specifically the form of male paternal care; Wingfield et al. 1990, 2000). Monogamous species in which males care for young are expected to show the largest increases in testosterone when challenges occur, because they normally maintain levels near the breeding baseline to avoid disrupting care. Polygynous species, by contrast, maintain elevated testosterone throughout the breeding season, because males provide less paternal care and face continual challenges. Their ability to elevate testosterone in response to acute challenges should thus be highly constrained. Again, these

predictions are generally upheld in a wide range of birds (Hirschenhauser et al. 2003, Wingfield et al. 2000).

Such interspecific comparisons are complicated, however, by the difficulty of monitoring short-term changes in testosterone (Goymann et al. 2007, Goymann 2009). Acute responses are sometimes assessed experimentally, through simulated territorial intrusions employing decoys (Goymann et al. 2007, Landys et al. 2007). In most studies, though, the response is estimated as the difference between the breeding baseline and the maximum levels observed during the breeding season. When these experimental and observational measures are both available, they are not correlated, across species (Goymann 2009).

For primates in the wild, experimental data comparable to those from the bird literature are currently lacking. The ease of resampling from known individuals, however, means that longitudinal hormone data can often be collected in reproductive and non-reproductive contexts, as well as with changes in social status that influence reproductive opportunities. In this paper I review the relationship between testosterone and mating effort in primates, with specific emphasis on the ways in which testosterone promotes male-male competition. I also explore the effects of testosterone on sexual behavior and social signaling. The emphasis throughout is on wild studies, as captivity can have large but unpredictable effects on both behavior and hormone production (e.g. Muller & Wrangham 2005). Captive data are discussed, however, when relevant data from the wild are unavailable.

The challenge hypothesis and mating competition in primates

Unlike birds, many primates are not seasonal breeders, and most do not engage in direct paternal care. Consequently, the predictions of the challenge hypothesis must be adapted for novel mating and breeding systems (e.g. Muller & Wrangham 2001, 2004). The underlying logic is that testosterone supports competitive behavior while imposing a range of predictable costs that animals are better off avoiding. Thus, elevated levels of testosterone are only expected during periods of social instability and heightened aggression. As with birds, aggression in primates is expected to intensify when males are defending territories (or other resources critical for reproduction), being directly challenged by other males, or guarding mates. Mating itself is not expected to cause substantial elevations in testosterone, unless accompanied by an increased risk of aggression.

Taking primate social and mating systems into account, the challenge hypothesis suggests multiple predictions. (1) In seasonally breeding primates, males should increase testosterone production during the mating season. These increases should be associated with male mating competition, rather than mating itself. (2) In non-seasonal breeders, males should increase testosterone production when competing for fecund females, and more intense competition should result in larger increases. Again, the association should be with increased aggression, rather than mating. (3) When little aggression occurs in mating contexts, but males compete aggressively to maintain long-term access to females (e.g. in species living in one-male groups), testosterone should increase primarily when males are threatened with losing access to females, rather than during mating periods. (4) When male status is importantly associated with mating access, and dependent on aggression, high-ranking males should

maintain higher testosterone levels than subordinates, particularly when dominance ranks are unstable, and being contested. (5) In territorial species, where territory size is importantly linked to reproduction, testosterone should increase during episodes of intergroup conflict. (6) From a life history perspective, males should show elevated testosterone during the parts of the lifespan in which they are competing most intensely for reproductive opportunities.

Prediction 1: Mating season increases in testosterone

Consistent with prediction 1, multiple studies of seasonally breeding primates report higher testosterone levels in the mating season than the non-mating season. These include three lemurs (*Lemur catta*: Cavigelli & Pereira 2000, Gould & Ziegler 2007; *Propithecus verreauxi*: Brockman et al. 2001; *Eulemur fulvus*: Ostner et al. 2002, 2008), golden lion tamarins (*Leontopithecus rosalia*: Bales et al. 2006), tufted capuchins (*Cebus apella*: Lynch et al. 2002), and four macaque species (Tibetan, *Macaca thibetana*: Xia et al. 2015; long-tailed, *Macaca fascicularis*: Girard-Buttoz et al. 2009, 2015; rhesus, *Macaca mulatta*: Mehlman et al. 1997, Higham et al. 2013a; Assamese, *Macaca assamensis*: Ostner et al. 2011). In two additional species - muriquis (*Brachyteles arachnoides*: Strier et al. 1999) and moustached tamarins (*Saguinus mystax*: Huck et al. 2005) – males did not increase testosterone during the mating season.

Are mating season rises in testosterone linked specifically to male mating competition? Unfortunately, some of the studies referenced above lack the behavioral data necessary to answer this question. For the remaining studies, results are mixed. Consistent with prediction 1, the two species that failed to show testosterone increases during the mating season, muriquis and moustached tamarins, also showed little or no aggression during that season (Huck et al. 2005, Strier et al. 1999). Further supporting prediction 1, ring-tailed lemurs, Assamese macaques, rhesus macaques, and long-tailed macaques all showed substantial increases in aggression during the mating season (Cavigelli & Pereira 2000, Gould & Ziegler 2007, Girard-Buttoz et al. 2015, Mehlman 1997, Ostner et al. 2011). For ring-tailed lemurs and Assamese macaques, individual rates of aggression and testosterone levels were correlated over the mating period (Cavigelli & Pereira 2000, Ostner et al. 2011). In long-tailed macaques, time spent mate-guarding, but not aggression, correlated positively with male androgen levels (Girard-Buttoz et al. 2015).

Contrary to prediction 1, three species – sifakas, redfronted lemurs, and tufted capuchins - showed elevated testosterone during the mating season without a corresponding increase in aggressive behavior (Brockman et al. 2001; Lynch et al. 2002, Ostner et al. 2002, 2008). Redfronted lemurs exhibited the most unusual pattern, with testosterone levels in the mating season higher than pre- and post-mating periods, but lower than levels in the birth season. The authors attribute this pattern to the need for males to defend their offspring from infanticide during the birth season, a possibility that is discussed further below (Ostner et al. 2002, 2008).

Across these studies, investigators considered a broad range of “non-mating” periods when making comparisons with the mating season. These included the birth season, the period of

lactation, the pre-mating period, and the post-mating period. How such choices influence the overall pattern of findings is not clear.

Prediction 2: Testosterone and mating competition in non-seasonal breeders

In many primates, the availability of cycling females is unpredictable, and males likely maintain breeding levels of testosterone throughout the year (e.g. Muller & Wrangham 2004). In these species, testosterone levels are predicted to rise when males are competing over cycling females. More intense competition should produce greater increases. Because males compete most intensely over the most fecund females (i.e. those with the highest probability of successful conception), testosterone increases are expected to correlate positively with female fecundity.

Consistent with prediction 2, male gray-cheeked mangabeys (*Lophocebus albigena*: Arlet et al. 2011), white-faced capuchins (*Cebus capucinus*: Schoof et al. 2014), and chimpanzees (*Pan troglodytes*: Muller & Wrangham 2004, Sobolewski et al. 2013) all showed elevated testosterone levels in the presence of periovulatory females (i.e. those most likely to conceive). In the same context, male chimpanzees and gray-cheeked mangabeys (Arlet et al. 2009) showed increased rates of aggression. Comparable data are not available for white-faced capuchins, though direct aggression over mating opportunities by males within groups is characterized as rare in this species (Jack & Fedigan 2005, Schoof et al. 2014).

Female bonobos (*Pan paniscus*) sometimes cycle for years before successful conception. In the presence of “potentially fertile females” (defined as estrous females in the 6 months prior to conception), however, male bonobos showed elevated levels of urinary testosterone (Surbeck et al. 2012). During the same periods they also showed increased rates of male-male aggression. The males that showed the largest testosterone increases, however, also showed the lowest mating rates. Additionally, high testosterone males showed lower rates of grooming with females. The authors suggest that in bonobos male-female affiliation, rather than male-male competition, is paramount in male mating success, and that testosterone may interfere with such affiliation. If true, this raises an interesting question of why low-ranking males increase testosterone production in this context.

The evidence that elevated testosterone is associated with male competition, rather than simply mating, is compelling for chimpanzees. Although males in Kanyawara (Kibale National Park, Uganda) mated with mothers and nulliparas at similar rates, mothers were more attractive, and generated more intense mating competition (Muller et al. 2006). Accordingly, males showed testosterone increases in the presence of estrous mothers, but not with nulliparous females (Muller & Wrangham 2004). This finding was replicated in a second community, also in Kibale National Park, at Ngogo (Sobolewski et al. 2013).

Studies of male baboons have focused on testosterone production during consortships, defined as periods when males mate-guard estrous females, maintaining close proximity and exclusive mating access (Seyfarth 1978). Yellow baboon (*Papio cynocephalus*: Onyango et al. 2013) males had higher levels of fecal testosterone in months when they obtained consortships than those in which they did not. Chacma baboon males (*Papio ursinus*) similarly increased testosterone production during consortships (Behner et al. 2006,

Kalbitzer et al. 2015), but this was not true for Guinea baboons (*Papio papio*: Kalbitzer et al. 2015). Behavioral differences among these species are consistent with prediction 2, as consortships in Guinea baboons are not distinguished by the elevated levels of aggression that characterize Chacma and yellow baboon mate guarding (Bergman et al. 2005, Kalbitzer et al. 2015).

Prediction 3: Reproductive challenges outside of the mating context

In some primates, the most important reproductive challenges faced by males occur outside of the mating context. These include species living in one-male groups, as well as groups that have strong alpha males who monopolize reproduction when females are receptive. In such species, testosterone is expected to increase when the stability of established groups is threatened, especially by outside males who lack access to females.

Consistent with prediction 3, in multiple species, established males show elevated testosterone production, along with increased rates of aggression, when extragroup males attempt to join or take over a group. These include mantled howler monkeys (*Alouatta palliata*: Cristóbal-Azkarate et al. 2006), white-faced capuchins (Schoof & Jack 2013), ursine colobus monkeys (*Colobus verosus*: Teichroeb & Sicotte 2008), gelada baboons (*Theropithecus gelada*: Pappano & Beehner 2014), and siamangs (*Symphalangus syndactylus*: Morino 2015). A similar pattern was documented experimentally in captive marmosets (*Callithrix kuhlii*: Ross et al. 2004). When resident male marmosets were exposed to unfamiliar intruders, their urinary testosterone levels increased in direct proportion to the amount of aggression directed at the intruder.

Black howler monkey males (*Alouatta pigra*), by contrast, showed no significant effect of either male immigration or encounters with extragroup males on testosterone production (Van Belle et al. 2009). Rangel-Negrín and colleagues (2011), however, reported that black howler males living in unimale groups had elevated testosterone levels, particularly after transitioning from multimale composition. They note that in black howlers, males in unimale groups are the most likely to be challenged and evicted by extragroup males. Thus, males living in multi-male groups are less likely to perceive encounters with extragroup males as salient challenges.

Prediction 4: Testosterone and male dominance rank

The logic of the challenge hypothesis suggests that positive associations between testosterone and male status should primarily be found when rank is (1) predictive of mating access, (2) maintained by aggression, and (3) unsettled (Muller & Wrangham 2004, Sapolsky 1993, Whitten 2000). When high-ranking males are not obliged to be more aggressive than others - either because the hierarchy is stable, or aggression does not influence mating success - then they should moderate testosterone production to avoid unnecessary costs.

In a number of primates, dominant males appear to consistently maintain higher testosterone levels than subordinates. These include sifakas (Brockman et al. 2001, Kraus et al. 1999), white-faced capuchins (Schoof et al. 2014, 2016), gray-cheeked mangabeys (Arelt et al. 2011), long-tailed macaques (Girard-Buttoz et al. 2015), mandrills (*Mandrillus sphinx*:

Setchell et al. 2008, Wickings & Dixson 1992), mountain gorillas (Robbins & Czekala 1997), and orangutans (Marty et al. 2015). In these species, high-ranking males are generally able to monopolize estrous females, particularly during the periovulatory period. As a consequence, they are likely to face chronic challenges. By contrast, persistent differences in testosterone production between high and low ranking males were not detected in studies of redfronted lemurs (Ostner et al. 2002, 2008), Assamese macaques (Ostner et al. 2011), and tufted capuchins (Lynch et al. 2002). Consistent with prediction 4, in these species, high-ranking males were not able to monopolize females, and mating success was similar for high- and low-ranking males.

Multiple studies have found an effect of dominance instability on the relationship between testosterone and male rank. In rhesus macaques (Higham et al. 2013a), chacma baboons (Beehner et al. 2006), and olive baboons (*Papio anubis*: Sapolsky 1983, 1993), testosterone and rank were unrelated, except during periods of instability, when high-ranking individuals had the highest levels of testosterone. In sifakas (Brockman et al. 2001) and bearded capuchins (*Sapajus libidinosus*: Mendonca-Furtado et al. 2014), dominant males residing in unstable groups had significantly higher testosterone levels than those living in stable groups. And in golden lion tamarins, dominant males maintained elevated androgen levels in the presence of unrelated subordinate males, but not when subordinates were relatives (Bales et al. 2006). Consistent with prediction 4, males had less stable relationships with non-relatives. No correlation was found between testosterone and dominance rank in ursine colobus monkeys during a period of rank stability (Teichroeb & Sicotte 2008).

In wild chimpanzees, positive associations between dominance rank and testosterone production have been found in some studies (Muehlenbein et al. 2004, Muller & Wrangham 2004), but not others (Sobolewski et al. 2013). The same is true for bonobos (cf. Marshall & Hohmann 2005, Surbeck et al. 2012). Whether this variation is explained by rank stability is not yet known.

In chacma baboons, Beehner et al. (2006) found that males rising in rank had higher testosterone than males falling in rank, and that testosterone was predictive of future rank. This is consistent with the idea that testosterone facilitates aggressive behaviors that subsequently enhance status. Evidence that testosterone rises or falls in response to success or failure in competitive interactions is discussed below.

Prediction 5: Testosterone and territoriality

Testosterone supports male territorial behavior in a number of birds, lizards, and mammals, when acquisition or expansion of a territory increases reproductive opportunities (e.g. Bartsh et al. 1992, Sinervo et al. 2000, Wingfield 1994). In one study of wild chimpanzees, males showed elevated testosterone levels prior to conducting territorial boundary patrols, and levels remained high during and immediately after patrols compared to control days (Sobolewski et al. 2012). In chimpanzees, territorial expansion increases male reproductive opportunities by shortening female birth intervals (Williams et al. 2004). These findings are consistent with prediction 5, but relevant data from other primates are lacking.

Prediction 6: Testosterone and male life history

From a life history perspective, the challenge hypothesis suggests that males should maintain elevated testosterone during parts of the lifespan in which they are competing most intensely for reproductive opportunities, with reduced levels during periods of development and senescence. This prediction is supported by observations of chacma, yellow, and gelada baboons, which all showed peak levels of testosterone at the age of first sexual consortship, and diminished production later in life, as mating access also declined (Beehner et al. 2009). Testosterone senescence occurred at a later age in yellow baboons, consistent with the fact that older, low-ranking males in that species enjoyed greater mating access than equivalent chacma or gelada males. In chimpanzees, males attain adult levels of testosterone production around age 15-16, which coincides with the period when they first challenge adult males for status (Figure 1). Peak testosterone levels occur around the age of maximum reproductive output, 17-18 (Muller et al. 2016ab). For chimpanzee males, a decline in testosterone production with advanced age is detectable, but both it and the age-specific decline in fertility are less steep than those in baboons (ibid.).

Predictions 1-6: Conclusions

Evidence from a broad range of primates thus supports the idea that testosterone is commonly elevated when males face reproductive challenges that require an aggressive response. The precise nature of such challenges is driven by the social and mating system. In species where male reproductive competition commonly occurs in mating contexts, testosterone rises during mating periods. In species where male-male aggression is less important in mating contexts, the relationship between testosterone and mating activity is less consistent.

Is some of the testosterone produced by males in mating contexts necessary to support spermatogenesis and sexual motivation? Although these are not well studied in the wild, captive data suggest that relatively low concentrations of circulating testosterone are generally adequate to maintain male reproductive function (Dixson 2012; for humans see Christiansen 2004, Weinbauer et al. 2004). Researchers consistently report, for example, that intact rhesus macaque males exposed to receptive females outside of the breeding season immediately exhibit normal sexual behavior; sustained increases in circulating testosterone occur subsequently (Bernstein et al. 1983, Michael & Zumppe 1993, Ruiz de Elvira et al. 1982). Castrated rhesus, by contrast, show a gradual decline in sexual behavior over time (reviewed in Dixson 2012). The evidence reviewed above is consistent with this kind of threshold effect being common. Muriquis, for example, exhibit extreme sperm competition, but fail to increase testosterone substantially during the mating season, during which they show little or no direct competition over access to females (Strier et al. 1999).

Testosterone and trade-offs between mating effort and paternal care

In a wide range of vertebrates, including birds, fish, anurans, and mammals (reviewed in Bales & Saltzman 2016; Lynn 2008, 2016; Marler et al. 2003; Wynne-Edwards 2001), associations between testosterone and paternal care are generally negative. In many species, experimental administration of testosterone actively suppresses paternal behavior (Clark &

Galef 1999; Lynn 2008, 2016). There are exceptions to this pattern, however, and they occur in predictable contexts. First, in species where paternal care is critical for male reproductive success, males can become insensitive to testosterone during periods of caregiving (Lynn 2008). Second, in species that must exhibit aggressive behavior and paternal care more or less simultaneously, paternal behavior may not be adversely impacted by testosterone (Marler et al. 2003, Trainor & Marler 2001). In some cases paternal behavior may even be promoted by testosterone, after its conversion to estrogen (Trainor & Marler 2002).

The challenge hypothesis was originally formulated for seasonally breeding birds. In many of these species, males invest heavily in parenting effort, both by incubating eggs and provisioning offspring. These activities directly conflict with mating effort, as time and energy devoted to them cannot be used to support, for example, territorial or courtship displays. Trade-offs between mating and parenting effort are not universal, however (reviewed in Stiver & Alonzo 2009). Some forms of mating effort involve behaviors that are compatible with parenting, and when this is true, elevated testosterone production is not expected to suppress paternal behavior. Once again, predictions of the challenge hypothesis must be adapted to fit primate mating and breeding systems (e.g. Salzman & Ziegler 2014).

Only a few primates invest in costly direct paternal care, such as carrying and provisioning offspring (Fernandez-Duque et al. 2009, Muller & Emery Thompson 2012). Among those that do, hormone data from the wild are rare. A clear trade-off between mating effort and parenting effort has been identified in black tufted-ear marmoset fathers (*Callithrix kuhlii*), who both carry infants and share food with them (Bales & Jarcho 2013, Storey & Ziegler 2016). In captive animals, significant declines in testosterone were observed 3-4 weeks following parturition, coinciding with the peak rate of infant carrying by fathers (Nunes et al. 2000). This effect was most pronounced in experienced fathers. Furthermore, across fathers, testosterone was negatively correlated with infant carrying (Nunes et al. 2001). Direct contact with infants is thought to be responsible for this pattern, as captive common marmosets (*Callithrix jacchus*) showed a drop in serum testosterone levels within 20 minutes of exposure to the scent of their infants (Prudom et al. 2008). Such detailed data are not available for golden lion tamarins, but wild males in that species are highly solicitous of infants, and maintained lower levels of testosterone during the birth and infant care season than the mating season (Bales et al. 2006).

Although cotton-top tamarin (*Saguinus oedipus*) fathers also carry infants and share food with them (Bales & Jarcho 2013), in captivity they increased testosterone production just prior to the birth of their infants (Ziegler et al. 2004). A similar pattern was observed in a wild population of moustached tamarins (Huck et al. 2005). Because tamarin females show postpartum ovulation, this likely represents a situation where males must be prepared to engage in paternal care and mating competition simultaneously (Storey & Ziegler 2016). Evidence of a trade-off remains, however, as captive cotton-top tamarin males without infants increased testosterone production when exposed to the scent of a periovulatory female, whereas fathers did not (Ziegler et al. 2005).

In humans, considerable evidence supports a trade-off between mating and parenting effort, partly mediated by testosterone (reviewed in Gettler 2014, Gray & Anderson 2010, Roney &

Gettler 2015, Storey & Ziegler 2016). For example, longitudinal studies reported that invested fathers decreased testosterone levels near parturition (Berg & Wynne-Edwards 2001, Storey et al. 2000). And a series of cross-sectional studies have variously shown that men in committed, long-term relationships, fathers, or both maintain lower levels of testosterone than unpaired men, or married men pursuing additional mates (e.g. Alvergne et al. 1999, Burnham et al. 2003, Gray & Campbell 2009, Gray et al. 2002, 2006, 2007ab; Hooper et al. 2011, Kuzawa et al. 2009, Muller et al. 2009). A longitudinal study from the Philippines demonstrated that this relationship likely results from men muting testosterone production in response to marriage and fatherhood, rather than low-testosterone men being more likely to marry and have children (Gettler et al. 2011). In various studies, men with elevated testosterone were found to be less responsive and less sympathetic to infant cries (Fleming et al. 2002), less interested in infants or infant stimuli (Roney et al. 2006, Storey et al. 2000, Weisman et al. 2014), and less involved with families and parenting (Alvergne et al. 2009, Mascaro et al. 2013). Further evidence for a link between androgens and men's mating effort comes from studies showing a positive association between testosterone and interest in extra-pair mating (Edelstein et al. 2011, McIntyre et al. 2006), incidence of extra-marital affairs (Booth & Dabbs 1993), and number of sexual partners (Bogaert & Fisher 1995, Peters et al. 2008, Pollet et al. 2011, van Anders et al. 2007). Finally, men who reported greater “interest in babies” had lower testosterone reactivity to cues of short-term mating (Zilioli et al. 2015).

In most primates the predominant form of direct paternal investment is not infant transport or provisioning, but physical protection – either from infanticide or predation (Muller & Emery Thompson 2012). Infanticide by male conspecifics is an important source of mortality in many species, particularly those living in one-male groups or groups with high reproductive skew (Palombit 2012). Because of their small body size, infants are also presumed to be at greater risk of predation than adults (Cheney & Wrangham 1987), though data are lacking for most species (for red colobus monkeys, *Colobus badius*, see Stanford 1998).

Male investment in infant defense is unlikely to conflict with mating effort for at least two reasons. First, there is some evidence that females in species at high risk for infanticide either abandon males who are unsuccessful at defending infants, or form preferential bonds with those who are effective defenders (Palombit 2009, 2012; Sterck & Korstjens 2000; Watts 1989). Consequently, male protection can simultaneously function as both mating and parenting effort (see Smuts & Gubernick 1992, van Schaik & Paul 1998). Second, substantial evidence supports the idea that testosterone facilitates aggressive male competition (reviewed below). Consequently, when paternal investment takes the form of aggression, testosterone should support that investment, rather than compromising it.

In several primates at high risk of infanticide, males show elevated testosterone in the period around parturition, when offspring are most vulnerable. These include redfronted lemurs (Ostner et al. 2002, 2008), sifakas (Brockman et al. 2001), and ursine colobus monkeys (Teichroeb & Sicotte 2008). Such increases have been argued to support aggression in the context of infant protection. A similar dynamic has been established experimentally in fish

that exhibit paternal care, with androgens promoting male nest defense from brood predators (e.g. Desjardins et al. 2008, Dey et al. 2010).

Multiple experimental studies have found that men respond to the sound of infant cries by increasing testosterone production (Fleming et al. 2002; Storey et al. 2000; van Anders et al. 2012, 2014). By contrast, when men hear infant cries while engaging in nurturant behavior, their testosterone levels decline (Kuo et al. 2015, van Anders et al. 2014). One interpretation of these results is that when men hear infant cries, but are unable to respond to them, cries are perceived as evidence of a threat to the infant that necessitates an aggressive, protective response (van Anders et al. 2011). Alternatively, testosterone increases in this context could result from men perceiving infant cries as a kind of social provocation (Kuo et al. 2015).

Yellow baboons have comparatively low rates of infanticide, but males in the wild selectively support their offspring in fights with conspecifics (Alberts 2012, Buchan et al. 2003). This kind of paternal investment appears to be important for infants, resulting in earlier maturation (Charpentier et al. 2008). In Amboseli, proximity between males and their offspring was closer than that between males and unrelated infants, though it was not clear which party was responsible for maintaining that relationship. Additionally, males showed a positive correlation between testosterone production and the number of immature offspring they had in the group (Onyango et al. 2013). Paternal care in this case thus appears to involve tolerance and aggressive defense, rather than nurturance.

Silverback gorillas in Karisoke show a similar pattern, in that they were found in closer proximity to infants than were other males in the group (Rosenbaum 2012). In this case the relationship was clearly driven by the infants, however, who were attracted to the silverbacks (ibid.). Again tolerance and protection, rather than direct nurturance, appears to be the paternal contribution. Perhaps for this reason, no relationship was found between fecal testosterone levels and male-infant social relationships in this population (Rosenbaum et al. 2016).

In combination, the baboon and gorilla data support the idea that testosterone can have both positive and negative effects on paternal care, depending on the form that such care takes. When care involves infant defense, or requires males to compete aggressively with other males, testosterone might act as promoter rather than inhibitor. When care takes the form of nurturance, however, or is otherwise hindered by mating effort, then testosterone should impede care (van Anders et al. 2011). Because infant defense represents the dominant form of paternal investment in the order, trade-offs between mating and parenting effort are likely to be weaker in most primates than in birds. Men represent an exception, as they provide more investment than other primate males, including forms of direct nurturance that are likely compromised by testosterone.

What is testosterone doing?

Although studies of wild primates indicate that male testosterone is often elevated during reproductive competition, the proximate relationship between aggression and testosterone is not well understood. In some studies testosterone shows strong correlations with aggression,

but in others it does not. One solution to this puzzle is that testosterone has both physiological and psychological effects that increase the probability of aggression between specific individuals, and in specific contexts, but without a direct causal link. Some of these effects have been studied in wild primates, but others are better documented in laboratory studies of humans and rodents. Here I briefly review testosterone's (1) psychological effects, (2) winner and loser effects, (3) analgesic effects, (4) effects on male armaments, (5) effects on male adornments, and (6) effects on male vocalizations. As we shall see, many of these effects plausibly provide an advantage in male mating competition.

Psychological effects

The psychological effects of testosterone have been best studied in humans, and are important to review here because of their relevance to status competition among primates generally (Eisenegger et al. 2011, Terburg & van Honk 2013). Numerous studies have found that testosterone is associated with the motivation to dominate others, and to avoid being dominated oneself (Grant & France 2001; Josephs et al. 2006; Mazur & Booth 1998; Schultheiss et al. 1999, 2003, 2005; Sellers et al. 2007; Stanton & Schultheiss 2009). Relatedly, testosterone appears to increase vigilance to signs of potential dominance behavior in others. For example, men with higher basal testosterone levels showed enhanced attention toward, and increased amygdala activation in response to, angry faces (Derntl et al. 2009, Stanton et al. 2009, van Honk et al. 1999, Wirth & Schultheiss 2007). Additionally, experimental testosterone administration decreased gaze aversion from, and increased both cardiac and amygdala reactivity to, angry faces (Hermans et al. 2008, Radke et al. 2015, Terburg et al. 2012, van Honk et al. 2001). Finally, among men who were chemically castrated, those receiving exogenous testosterone showed greater amygdala reactivity to angry faces than those receiving placebo (Goetz et al. 2014). Comparable data are not available from non-human primates. Captive rhesus macaques that were given exogenous testosterone significantly increased their time spent watching video clips of fights between unfamiliar conspecifics, however, suggesting equivalent effects (Kelly et al. 2014, Lacreuse et al. 2010).

Testosterone has the additional action, in a range of species, of reducing fear and anxiety in both social and non-social contexts. Animals treated with testosterone have shown reductions in fear-related behaviors in response to diverse stimuli, including isolation from conspecifics, human approach, unfamiliar environments, novel objects, and surprising events (rodents: Aikey et al. 2002, Fernandez-Guasti & Martinez-Mota 2005, Frye & Seliga 2001, Hodosy et al. 2012, Raynaud & Schradin 2014; cattle: Boissy & Bouissou 1994; sheep: Bouissou & Vandenheede 1996). Experimentally lowering testosterone levels has the opposite effect, increasing fear-related behaviors (King et al. 2005). Similar results have been documented in multiple human studies (e.g. Enter et al. 2014; Hermans et al. 2006, 2007; van Honk et al. 2005).

Data from non-human primates are again rare, but captive studies of rhesus macaques show mixed results. Consistent with the fear-reducing effects of testosterone in other species, monkeys who were gonadectomized spent less time in association with unfamiliar conspecifics than did intact animals, and took longer to retrieve food placed under the image

of a threatening monkey face (Richards et al. 2009). Testosterone administration caused older, but not younger, monkeys to spend more time in proximity to unfamiliar objects (Kelly et al. 2014). By contrast, monkeys whose testosterone levels were lowered through pharmacological castration did not show increased anxiety (Lacreuse et al 2010, 2012), or even showed reduced anxiety (Suarez-Jimenez et al. 2013). This discrepancy may be explained by the fact that the GnRH agonist used to shut down testosterone production in these studies itself has fear-reducing properties (Suarez-Jimenez et al. 2013).

In a range of species, then, testosterone appears to increase the desire for high status, enhance sensitivity to status threats, and decrease fear in the face of such threats. All of these effects presumably increase the odds of successful aggression in contexts where status is threatened (reviewed in Eisenegger et al. 2011, Montoya et al. 2012, Oliveira & Oliveira 2014, Terburg & van Honk 2013).

Winner and loser effects

Experience in aggressive contests influences both the likelihood of engaging in and the outcome of future contests, with recent winners more likely to compete and win, and recent losers more likely to withdraw or lose (reviewed in Hsu et al. 2006). One prominent hypothesis for these effects involves self-assessment. If an individual is uncertain of its relative fighting ability, then the best strategy is to modulate aggression in response to the outcome of recent contests (Fawcett & Johnstone 2010, Rutte et al. 2006). Winning fights should, all else being equal, lead to increased aggression, and losing fights should lead to avoidance of further competition.

Evidence from a range of species suggests that testosterone is often involved in modulating competitive responses to winning and losing (Gleason et al. 2009). Winner effects are particularly well studied in California mice (*Peromyscus californicus*). Males in this species show acute increases in testosterone after winning aggressive encounters with intruder males. This testosterone response produces a shorter attack latency and increased likelihood of winning in future interactions, effects that disappear when the response is experimentally blocked (Fuxjager et al. 2011a, Oyegbile & Marler 2005, Trainor & Marler 2001, Trainor et al. 2004). In a closely related species, the white-footed mouse (*Peromyscus leucopus*), winning produces neither a rise in testosterone, nor an increase in the probability of winning future fights. When an exogenous testosterone surge is administered in response to victory, however, this species shows a subsequent winner effect (Fuxjager et al. 2011b). Similar dynamics have been documented in cichlid fish (Oliveira et al. 2009).

Loser effects, in which losing a conflict leads to an acute decline in testosterone, and a corresponding decrease in the probability of engaging in future aggression, are less well studied. In some species loser effects appear to be independent of androgen production. In the Mozambique tilapia (*Oreochromis mossambicus*), for example, loser effects were apparent even when losing was accompanied by an experimental testosterone increase (Oliveira et al. 2009). By contrast, administering testosterone to losers reversed the effect in Japanese quail (Hirschenhauser et al. 2013). And in mangrove killifish (*Kryptolebias marmoratus*), males with lower testosterone levels showed a stronger and longer lasting effect of losing than males with higher levels (Earley et al. 2013).

Humans show evidence of both winner and loser effects that are influenced by testosterone (Carré & Olmstead 2015). In multiple competitive contexts it is common for winners to show increases in testosterone, losers to show decreases, or both (reviewed in Archer 2006, Carré & Olmstead 2015, Oliveira & Oliveira 2014). Not all studies find these effects; important moderating factors include whether outcomes are (1) decisive, (2) attributed to individual effort (rather than chance or the effort of others), and (3) interpreted as salient to an individual's status (Carré 2009, Edwards et al. 2006, Gonzalez-Bono et al. 2000, Mehta et al. 2015, Casto & Edwards 2016). In one experimental study, losing combined with a decrease in testosterone made participants less likely to engage in future competition (Mehta & Josephs 2006). In additional studies, testosterone increases in response to winning predicted performance in, or the decision to participate in, later contests (Carré & McCormick 2008, Zilioli & Watson 2014). Acute rises in testosterone in response to winning also produced increases in subsequent aggressive behavior (Carré et al. 2011, 2013).

Captive data suggest that rhesus macaques living in unstable social groups show testosterone increases after winning aggressive encounters, and declines after losing (Bernstein et al. 1974; Rose et al. 1972, 1975). Winner and loser effects are generally understudied in non-human primates, however, particularly in the wild. One significant impediment to such research involves the ephemeral nature of potentially important endocrine responses. For example, in mouse studies, an acute rise in testosterone that lasts for only 40 minutes can affect subsequent competitive behavior over a period of 2-6 days (Gleason et al. 2009). Frequent urine sampling might enable detection of acute hormone shifts in wild primates that could be correlated with winning and losing, but most experimental approaches are prohibitively invasive.

Analgesic effects

If testosterone increases the probability of aggressive behavior, then it also increases the potential for injury. The perception of pain, in turn, is likely to interfere with effective aggression (Hau et al. 2004). Consequently, one of testosterone's effects is to decrease pain perception. Experimental studies in birds, rats, and mice have shown that blocking the action of testosterone increases sensitivity to painful stimuli, while testosterone administration decreases it (Craft et al. 2004, Hau et al. 2004).

In humans, substantial evidence suggests that women are more sensitive than men to multiple forms of pain, and sex differences in testosterone have been invoked to explain this difference (Fillingim et al. 2009, Mogil 2012, Racine et al. 2012). Consistent with this hypothesis, sensitivity to painful stimuli was negatively correlated with salivary testosterone in a sample of U.S. women (Bartley et al. 2015). Additionally, men with androgen deficiency exhibited greater tolerance to multiple forms of induced pain after treatment with exogenous testosterone (Basaria et al. 2015). Data from non-human primates are again lacking.

Effects on male armaments: sexually dimorphic musculature

Testosterone frequently supports the secondary sexual characteristics that males use as armaments in reproductive competition (Hau 2007). In red deer (*Cervus elaphus*), for example, androgens control the seasonal growth and development of male antlers, together with the sexually dimorphic neck musculature that powers them (Fletcher 1978, Li et al. 2003, Lincoln et al. 1972). For most primates, sexually dimorphic canines and musculature are the main weapons in male-male competition (Mitani et al. 1996, Plavcan 2004). Little is known about the relationship between testosterone and canine growth, but in captive rhesus macaques, experimental prenatal testosterone exposure increased both the developmental rate and adult size of canine teeth (Hurme & van Wagenen 1956, Zingesser & Phoenix 1978). By contrast, the effects of testosterone on sexually dimorphic musculature are well studied (e.g. Bhasin et al. 2004).

Both acute and chronic effects of testosterone on muscle tissue have been investigated. Sapolsky (1993) hypothesized that the acute, transient elevations in testosterone that accompany competition might have immediate metabolic effects on muscle that would provide an advantage in fights or chases (see also Crewther et al. 2011). This idea is ostensibly supported by in vitro studies showing that testosterone causes rapid increases in glucose uptake and calcium release in muscle cells (Estrada et al. 2000, 2003, Tsai & Sapolsky 1996). In vivo support has proven elusive, however. Androgen treatments in vivo had no immediate effect on the maximal force, power or fatigue resistance of muscles in mice, nor on their evoked calcium transient (Frayssse et al. 2014). And in humans, a series of careful studies have found no effect of acute, exercise-induced increases in men's testosterone on muscular performance, growth, or strength, either during or postexercise (West et al. 2009, 2010, 2012; West & Phillips 2012). More studies are needed, however, and surprises are possible.

Chronic effects of testosterone on muscle development in primates are better established. For example, experimental administration of testosterone increased muscle mass in captive long-tailed macaques (Weinbauer et al. 2003). And in captive studies of male baboons, pig-tailed macaques, and rhesus macaques, serum testosterone levels correlated positively with upper-arm circumference, a proxy for muscle mass, after controlling for age (Muehlenbein et al. 2001, 2002). The only comparable wild data come from long-term studies of chimpanzees in which urinary creatinine served as a proxy for musculature (Emery Thompson et al. 2012, Muller et al. 2016a). Creatinine is produced at a relatively constant rate by skeletal muscle, and in humans correlates with measures of lean mass (e.g. Baxmann et al. 2008, Jassal et al. 2015). Male chimpanzees in Kanyawara, Kibale National Park, showed positive correlations between concentrations of urinary creatinine and testosterone (Figure 2; Emery Thompson et al. 2012, Muller et al. 2016a).

In humans, administering supraphysiological doses of testosterone produces increases in muscle size and strength, as does providing testosterone supplementation to hypogonadal men (Bhasin et al. 2004). Modulating testosterone levels within the broad normal range, however, does not have clear effects on lean mass (Bhasin et al. 1998, 2004). Consequently, direct correlations between testosterone and measures of musculature in adult men are generally modest or nonexistent (reviewed in Alvarado et al. 2015).

Humans differ from most primates, though, in that sexually dimorphic musculature is important not only for male-male competition, but for parenting effort. In foraging and other small-scale societies, men often provision their families through work that requires episodic bursts of upper-body strength (Murdock & Provost 1973). Workload increases with the number of dependents (e.g. Hooper 2011, Wood & Marlowe 2013). As previously discussed, invested human fathers typically curtail testosterone production, probably to avoid trade-offs with increased mating effort. Consequently, a tight link between testosterone and muscle maintenance in men would not be adaptive, because falling testosterone during fatherhood would compromise men's physical abilities when they are most important for family provisioning (Alvarado et al. 2015).

Alvarado and colleagues (2015) hypothesize that strength and musculature in men should be more sensitive to physical demand, and less sensitive to changes in circulating testosterone, than in other primates. This prediction is supported by data from rural Poland, where fathers maintained lower levels of salivary testosterone than non-fathers, but greater labor demands, strength, and musculature (Alvarado et al. 2015). Within individuals, testosterone levels were lowest during the harvest season, when men performed heavy labor and showed increased muscle mass, and highest during the winter, when workloads were low and muscle mass decreased (Alvarado et al. 2016). Further support comes from direct comparisons of the relationship between testosterone and creatinine production in chimpanzees and Tsimane forager-horticulturalists. Although there is a weak, positive relationship between testosterone and creatinine in Tsimane men, testosterone accounts for half as much variance in urinary creatinine in that population as it does in wild chimpanzees (Muller et al. 2016a).

Effects on male adornments

Across primates, the presence of striking secondary sexual adornments, such as beards, capes, crests, cheek pads, and color patches, is strongly associated with a polygynous mating system (Dixson 2005). Many of these traits appear to function as badges of status, signaling the competitive abilities of the bearer (Dixson 2012). Badges are distinct from armaments, such as canines and musculature, in that they confer no direct advantage in fighting. Rather, in species with intense reproductive competition, where males risk injury in fights, such signals help to settle potentially dangerous encounters before they escalate (Senar 2006, Whiting et al. 2003). Sexually dimorphic adornments are most common in primate species maintaining large groups and multilevel social organization (Grueter et al. 2015). Status badges are likely to be beneficial in such complex societies, because competition is common, and animals have increased difficulty identifying individuals and tracking their competitive abilities (ibid.).

Although status badges generally evolve in the context of male-male competition, females in some species subsequently use them as indicators of male quality (Berglund et al. 1996). Consequently, male-male competition and female choice can both contribute as selective factors, but male-male competition is usually the initiating process. Experimental studies in both birds (e.g. Buchanan et al. 2003, Evans et al. 2000, Senar 2006), and lizards (Cooper et al. 1987; Cox et al. 2005, 2008; Salvador et al. 1996) indicate that testosterone often plays a direct physiological role in the development and maintenance of status badges. This

relationship makes sense, because badges only function if they reliably signal an animal's fighting ability or aggressive motivation, and testosterone is closely associated with these (McGlothlin et al. 2008). The numerous costs imposed by increased testosterone production help to ensure that any testosterone-driven signal is honest.

Captive work with primates indicates that a threshold level of testosterone is necessary for the development of many male secondary sexual traits. Castration of male hamadryas baboons, for example, results in the loss of the long white shoulder cape, whereas exogenous testosterone administration restores it (Zuckerman & Parkes 1939). Castration similarly causes red coloration to fade in the sexual skins of male rhesus monkeys, hamadryas baboons, and patas monkeys (*Erythrocebus patas*) (Dixson 2012, Vandenbergh 1965, Zuckerman & Parkes 1939). Evidence for a direct, dose-dependent relationship between testosterone and the expression of such traits, however, is harder to come by.

The clearest primate evidence linking testosterone with changes in both color badges and competitive abilities comes from mandrills (reviewed in Setchell 2016). Male mandrills maintain red patches on the face and genitals that are sensitive to social status. For example, in a semi-free-ranging colony, males who fell in rank subsequently lost color, and those who rose in rank gained it (Setchell & Dixson 2001). Males became redder over periods of dominance instability, and during competition for estrous females (Setchell et al. 2008). Similarly-colored males were the most likely to threaten or fight each other, whereas pale males submitted to those with darker coloration (Setchell & Wickings 2005). Finally, in all of these cases, red coloration was correlated with fecal androgen levels, which changed in concert with color (Setchell et al. 2008).

In a study of wild gelada baboons, dominance status was similarly communicated by the redness of male chest patches (Bergman et al. 2009). Leader males had the reddest chests, and among leader males, those whose groups contained more females had redder chests still. Following group takeovers, males who lost females lost redness, and those who gained females grew redder (ibid.). Although the relationship between testosterone and red coloration in geladas has not been directly examined, coloration in bachelor males does not change until after a successful challenge, despite the fact that males show clear rises in testosterone prior to making a challenge (Pappano & Beehner 2014). Thus, it seems unlikely that the relationship between testosterone and coloration in geladas is as straightforward as in mandrills (see discussion in Higham et al. 2013b). In semi-free-ranging drills (*Mandrillus leucophaeus*), male coloration was found to signal status in a manner equivalent to that described for mandrills (Marty et al. 2009), but testosterone measures are again lacking.

Male rhesus macaques express red coloration on their faces, rumps, and genitals during the mating season (Baulu 1976), and in captive studies, females attend more to red-faced than pale-faced males (Waitt et al. 2003). As previously noted, castration led to declines in male sex-skin coloration (Vandenbergh 1965). Low doses of exogenous testosterone restored the coloration seen in nonbreeding males, and high doses produced the coloration of breeding males (Vandenbergh 1965; see also Rhodes et al. 1997). Studies with free-ranging, provisioned monkeys on Cayo Santiago, however, found no correlation between color, and either rank or testosterone production during the breeding season (Higham et al. 2013b).

Females in this population showed clear preferences for dark red males over pale pink ones, however, suggesting that red coloration in rhesus males may currently be supported by female choice rather than male-male competition (Dubuc et al. 2014).

Less is known about the relationship between testosterone and non-color adornments in male primates. Adult male orangutans exhibit two morphs, only one of which possesses the suite of secondary sexual characteristics that includes projecting cheek pads, a throat pouch, long hair, and a musky odor (Knott & Kahlenbeg 2007). These dominant males exhibit higher androgen levels than undeveloped males, but further details are not available (Marty et al. 2015). Sifaka males also exhibit two morphs – one with a dark chest stain that is associated with sternal gland activity and scent marking, and one with a clean chest. Males with stained chests are the dominant males in multimale social groups, or the only adult males in single-male groups (Lewis & van Schaik 2007). Preliminary evidence shows that stained males have higher testosterone levels than clean males (Lewis 2009). In most species, though, relationships between testosterone, competition, and male adornments have yet to be examined in detail.

Effects on male vocalizations

In a number of anurans, birds, and rodents, testosterone regulates the production of vocalizations that males use to attract mates or repel sexual rivals (anurans: Marler & Ryan 1996, Solís & Penna 1997, Townsend & Moger 1987, Wilczynski et al. 2005; birds: Boseret et al. 2006, Harding 1991, Ketterson et al. 1992, McDonald et al. 2001, Nowicki & Ball 1989; rodents: Floody et al. 1979, Floody 1981, Kapusta & Pochro 2011, Pasch et al. 2011). In some species testosterone has short-term, activational effects on the motivation to vocalize. In others, testosterone alters the acoustic structure of vocalizations through its long-term effects on the organs of vocal production. As with visual badges of status, vocalizations can provide valuable information to both rivals and mating partners. Among primates, loud calls in particular incur energetic costs that potentially make them honest signals of male quality, and provide cues to male condition (reviewed in Delgado 2006).

The relationship between testosterone and rates of loud calling has been examined in several primates, with mixed results. In a study of captive mouse lemurs (*Microcebus murinus*), castration reduced calling, but rates were not influenced by natural variation in circulating testosterone (Zimmermann 1996). Similarly, the rate of long-distance calling in wild male black howler monkeys was not affected by testosterone production (Rangel-Negrín et al. 2011). In male chimpanzees, however, mean monthly testosterone levels correlated with mean monthly rates of pant-hooting, and diurnal patterns of pant-hooting paralleled those of testosterone production (Fedurek et al. 2016). Comparable data are not available from orangutans, but in that species loud calls are only produced by dominant, flanged males (Mitani 1985), who maintain higher androgen levels than unflanged males (Marty et al. 2015). Harem-holding gelada baboon males give loud calls during competitive displays against bachelor males. In one study, high-testosterone gelada males gave more loud calls than low-testosterone males, and calling rates were elevated during months when testosterone levels were the highest (Benitez et al. 2015). High-ranking yellow baboon and crested macaque males (*Macaca nigra*) also produce loud calls at higher rates than low-

ranking males (Kitchen 2003, Neumann et al. 2010), but a direct link with testosterone has not been investigated.

The evidence that testosterone affects the acoustic structure of primate calls is similarly mixed. In a study of Thomas langurs (*Presbytis thomasi*), several aspects of loud calls differed between life phases, but these did not correspond with changes in testosterone production (Wich et al. 2003). In white handed gibbons (*Hylobates lar*), by contrast, males with higher androgen levels produced songs of higher pitch (Barelli et al. 2013). In chimpanzees, males with higher testosterone levels produced pant-hoots with higher peak frequencies at the beginning of the climax (Fedurek et al. 2016). And in rhesus macaques, preliminary data suggested a positive association between androgen levels and acoustic frequency of male barks (Higham et al. 2013b). Higher frequency calls were also recorded in dominant yellow baboon males, but the relationship with testosterone was not examined (Fischer et al. 2004).

The association between high frequency calls and testosterone seems unusual, given that large body size is associated with low vocal tract resonant frequencies, and males in some species decrease these frequencies to exaggerate their formidability (Fitch & Reby 2001). In human men, for example, testosterone lengthens and thickens the vocal cords, causing lower voice pitch, which increases perceived social dominance (Apicella & Feinberg 2009, Archer 2006, Dabbs & Mallinger 1999, Hodges-Simeon et al. 2014, Puts et al. 2014). However, in some mammals, loud calls with high fundamental frequencies signal fitness and fighting ability (Garcia et al. 2013, Reby & McComb 2003, Reby et al. 2010). This is likely because producing loud, high-frequency calls requires intense lung pressure and large muscular effort that individuals low in strength or endurance cannot generate (Titze & Riede 2010). As was the case with male adornments, the relationship between loud calling and testosterone is one that needs further development in wild primates.

Future directions and conclusions

Much of the published research on testosterone and primate behavior employs either cross-sectional data, or longitudinal data that are limited to a single field season. Moving forward, an important goal is to track hormonal variation within individuals over longer periods. Primate research has a clear advantage here over bird studies, in that researchers sometimes observe known individuals over years or even decades. Such data are currently being collected in many species, and should help to answer questions raised in the preceding review. For example, how strong is the association between testosterone and the expression of ornaments (such as chest patches) or armaments (such as sexually dimorphic musculature) within individuals, and what factors affect the strength of that relationship? Why do mandrills show a robust relationship between red coloration and testosterone, whereas rhesus macaques do not (see Higham et al. 2013b for discussion)? Do levels of testosterone during adolescence predict aspects of morphology or behavior in adulthood? How does victory or defeat in an aggressive encounter affect subsequent testosterone production and dominance striving? How does testosterone change when males leave their natal groups, enter new groups, or attempt to take over new groups? And how do

reproductive tactics and testosterone profiles change during senescence? Detailed, longitudinal data are necessary to answer such questions.

Another valuable endeavor will be to collect similar longitudinal data from human populations. Even in anthropology, human studies have mostly followed an epidemiological strategy of targeting large numbers of subjects, but with limited hormone measures on each. Hormones are generally sampled cross-sectionally or, if longitudinally, once every few years. Having more detailed data on smaller samples of humans, together with matching behavioral and demographic data, will provide a valuable point of comparison with non-human primates, for whom truly large sample sizes will never be available.

Most of the work on testosterone and aggression in primates looks at reproductive competition among males. Much less is known about the relationship between testosterone and intersexual competition. In recent years the literature on sexual coercion and male aggression against females in primates has grown considerably (Muller & Wrangham 2009), and an important next step will be to look at hormonal aspects of these relationships. Although a few studies have examined the relationship between testosterone and partner abuse in humans (e.g. Soler et al. 2000), comparable data from non-human primates are lacking.

Similarly, work on the relationship between testosterone and intergroup competition in primates is mostly absent. Recent human data suggest that testosterone might simultaneously promote in-group bonds while increasing between-group hostility (Diekhof et al. 2014). Species exhibiting cooperative territorial behavior should provide opportunities for investigating this dynamic.

The relationship between testosterone and immune function in primates is another important topic for future research. Although testosterone is often characterized as immunosuppressive, the evidence for such an effect is mixed. Some studies actually show positive associations between testosterone and measures of immune function (e.g. Gettler et al. 2014). Additionally, in studies that report a negative relationship, it is not usually clear whether testosterone is suppressing the immune system directly or indirectly (for example, by channeling energy into mating effort at the expense of immune function; Muehlenbein & Bribiescas 2005). Still other studies indicate that testosterone is not universally immunosuppressive, but has positive or negative effects on different aspects of the immune system (Ezenwa et al. 2012).

Progress in this area will require better non-invasive methods to assay immune function in the wild (e.g. Higham et al. 2015, Heistermann & Higham 2015). Most studies employ a proxy for immune function, such as parasite load, to examine this relationship. Wild gray-cheeked mangabeys, for example, showed a positive relationship between nematode infection and fecal testosterone levels (Arlet et al. 2015), and high-ranking male chimpanzees exhibited both higher parasite richness (specifically the number of unique helminth species) and fecal testosterone levels (Muehlenbein & Watts 2010). It is not clear from such studies, however, whether this relationship is driven by variation in immune function, or by other potential factors, such as exposure. In support of the latter hypothesis,

social network analyses in one wild chimpanzee population showed that high-ranking males were more central, and thus more likely to be exposed to diverse pathogens (Rushmore et al. 2013, 2014). Prall and Muehlenbein (2014) review major issues and methodological concerns in this area.

The preceding review suggests that if testosterone does have direct, adaptive effects on immune function, then they are likely to be associated in some way with aggressive competition. This logic underlies the “immune redistribution hypothesis,” which proposes that high levels of testosterone temporarily shift immune cells to lymph nodes, skin, and other tissues “well positioned to combat challenges from new trauma” associated with aggression (Braude et al. 1999: 347). Regardless of whether this particular hypothesis is ultimately refuted, it represents a useful theoretical approach in considering specific aspects of immune function that should be positively or negatively impacted by testosterone.

Little has been said here about the technical issues surrounding hormone measurement, but it is possible that some of the conflicting findings discussed above result from differences in methodology. For example, it is clear that different species metabolize hormones differently, ultimately excreting testosterone as a range of metabolites, and at varying amounts in urine versus feces (Möhle et al. 2002). Consequently, the percentage of circulating testosterone recovered by an assay will depend on both the assay medium, and how closely the dominant metabolites are targeted by a specific antibody. Further, antibodies to testosterone generally show some cross-reactivity with other androgens. Thus, some studies purporting to measure testosterone may be primarily assaying related steroid molecules that show a different affinity for the androgen receptor. The choice of blood, urine, saliva, or feces as a medium will also affect the duration of hormone release over which one is sampling. Higham (2016) and Gray and colleagues (2016) provide current reviews of these and other methodological issues in hormone measurement. A clear message from these is that researchers should do more to ensure that they are measuring the hormones they claim to be measuring, and in ways that are comparable across studies.

Although less frequently discussed, similar problems are evident in the measurement of aggression. What counts as an aggressive behavior, and how rates of aggression are calculated vary substantially across studies and study species. Many researchers provide only cursory descriptions of their behavioral measures, however, so the scale of the problem is difficult to assess. Increased attention to this issue would undoubtedly facilitate more accurate comparisons across species and study sites.

In summary, the evidence reviewed above supports the role of testosterone as a mediator of life-history trade-offs in primates. Testosterone generally promotes mating effort at the expense of parenting effort or survival, especially when mating involves aggressive competition. Testosterone supports male competition through its psychological effects on status striving and competitive motivation, its analgesic effects, and its effects on the development and maintenance of male ornaments and armaments. When parenting effort takes the form of physical protection, however, rather than nurturant behaviors, then a stark trade-off between mating and parenting effort may not exist. This appears to be the case for most primates, with humans a prominent exception.

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Highlights

- Testosterone promotes mating effort in primates, at the expense of survival.
- In primates testosterone primarily facilitates aggression in reproductive contexts.
- Trade-offs between parenting effort and mating effort are weak in most primates.
- Testosterone's psychological and physiological effects promote male competition.

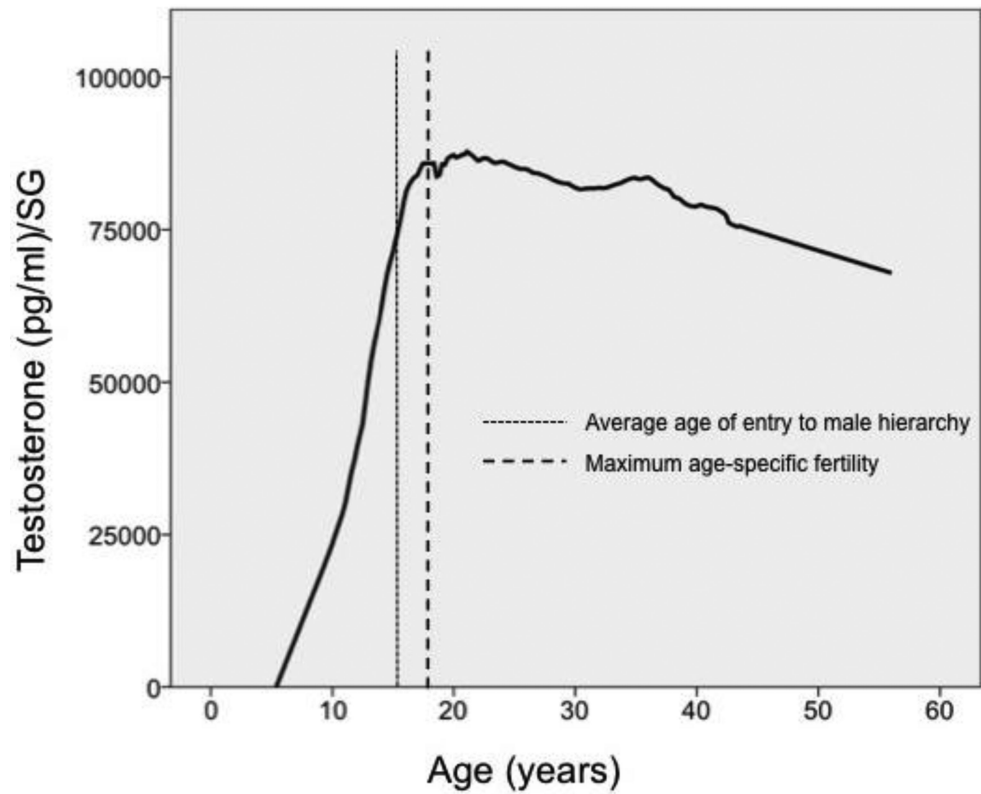


Figure 1. Testosterone, age, and reproductive effort in wild chimpanzees (Kanyawara, Kibale National Park). The trend line is a LOESS curve through 138 yearly means from 20 unique males. Each mean included a minimum of 20 observations from the male at that age ($n=6692$ total urine samples). Specific gravity (SG) is used to correct for urinary dilution. Point of entry in the adult male hierarchy represents the age that a male was first seen to win an aggressive interaction with an adult male.

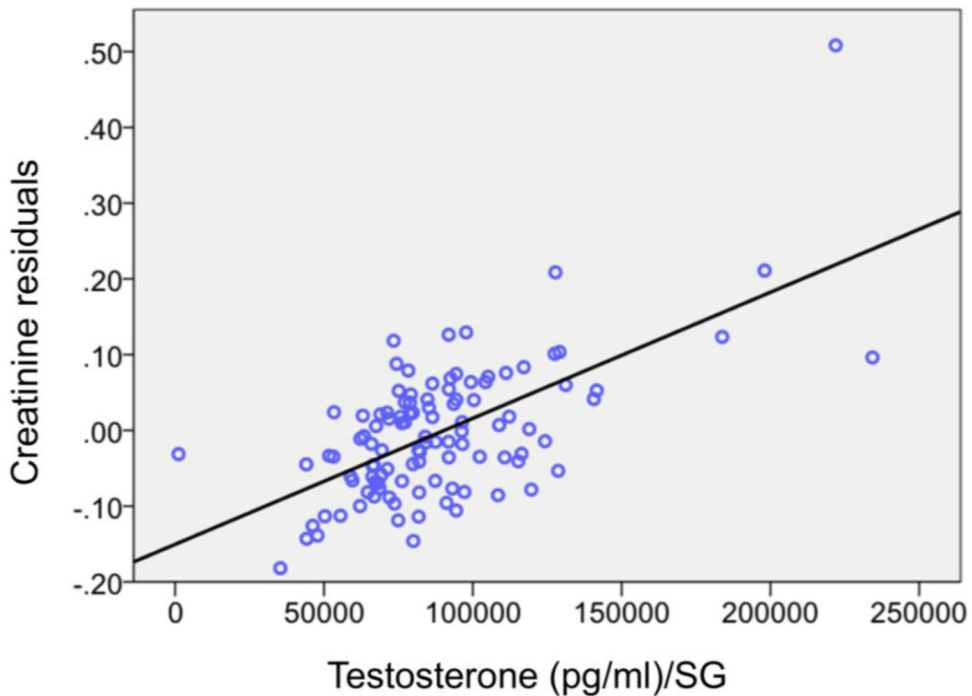


Figure 2.

Urinary testosterone levels correlated positively ($r=0.63$, $p<0.001$) with urinary creatinine, a proxy for skeletal muscle mass, in wild chimpanzees (Kanyawara, Kibale National Park). Each point ($n=112$) represents observations averaged over one year from one adult male ($n=16$ unique males). The x-axis shows mean yearly testosterone, corrected for specific gravity. The y-axis shows the unstandardized residuals of the regression of creatinine on specific gravity. Specific gravity (SG) is used to correct for urinary dilution. In humans, the relationship between creatinine and testosterone appears to be weaker than that observed in chimpanzees (see Emery Thompson et al. 2012, Muller et al. 2016a). The Kanyawara data include 6725 urine samples. Each point comprises a minimum of 20, and a mean of 60 samples.