

Hormonal Correlates of Dominance

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Despite being potentially costly in terms of time and resources, engaging in competition for dominance rank is a common occurrence in many species, including most primates. Such interactions include antagonistic physical aggression as well as manipulating and building alliances to gain favor within a social group. Attaining and maintaining high dominance rank can have many benefits, including increased access to food or other resources, increased social support, grooming benefits, and better access to mates and mating opportunities. From an evolutionary perspective, increased status within the dominance hierarchy can increase reproductive success. Dominance interactions may take place in both males and females, dependent upon the species in question and its particular socioecological conditions.

A preponderance of evidence from many species indicates that certain hormones both influence and are reactive to the formation and maintenance of dominance hierarchies. In particular, the hormone testosterone is well studied for its probable roles in dominance and aggression and its well-established roles in development and reproduction. As an anabolic-androgenic compound, testosterone affects body size, muscle mass, adiposity, and the development of other secondary sexual characteristics. Testosterone may influence the outcome of dominance interactions by stimulating muscle anabolism (through increased protein synthesis and glucose uptake into muscle tissue) and fat catabolism, aiding in both intrasexual competition and mate attraction. Evidence from rodent studies shows that, neurologically, testosterone shortens the refractory period of action potentials along the stria terminalis between the amygdala and

hypothalamus (Kendrick and Drewett 1979), thus potentiating aggressive behaviors following appropriate stimuli.

Given testosterone's physiological roles, it is unsurprising that early studies involving primates identified some support for the hypothesis that testosterone influences dominance rank. For example, higher-ranking rhesus macaque males were shown to have higher testosterone concentrations (Rose, Holaday, and Bernstein 1971), and such results have been replicated in other, but not all, primate species. These discrepancies may result from several factors. First, maintaining high testosterone concentrations can be physiologically costly, given the increased metabolic demands of maintaining energetically expensive skeletal muscle tissue and the hormone's immunosuppressive effects (Muehlenbein and Bribiescas 2005). Because of such costs, it is, in theory, advantageous to increase testosterone levels only when the benefits of doing so outweigh the physiological impacts. Such a situation might occur during the breeding season or in the presence of receptive females when reproductive competition is highest (the "challenge hypothesis;" Wingfield et al. 1990).

Testosterone likely facilitates the probability of agonistic behaviors relative to specific environmental and social conditions. For example, a classic study of talapoin monkeys (*Miopithecus talapoin*) found that gonadectomized males treated with testosterone increased their aggressive behaviors toward subordinate males, but not toward more dominant males (Dixon and Herbert 1977). In ring-tailed lemurs (*Lemur catta*), relationships between aggression and testosterone concentration are only found during mating periods (Cavigelli and Pereira 2000). However, in other species, high-ranking males may consistently demonstrate elevated testosterone levels relative to other males in anticipation of within-group agonistic interactions or extragroup male encounters. For example, in chimpanzees (*Pan troglodytes*), a species that engages in frequent agonistic interactions as part of a fission-fusion social system, testosterone is positively associated with dominance rank

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(Muehlenbein, Watts, and Whitten 2004). Therefore testosterone–dominance relationships are unique to the social situation of the individual species, and vary with changes in group stability, group composition, access to receptive females, and the possibility of in-group and out-group competitive interactions. Under these circumstances, testosterone in males may rise to facilitate physical competition, redirecting energy toward skeletal muscle and altering neural circuitry to catalyze the occurrence of agonistic behaviors.

Less is known about the relationships between dominance and hormones in female primates. Females secrete testosterone from the adrenal glands (while it is produced primarily in the testes in males), and variation among females in testosterone has been associated with reproductive status in some species. For example, in a population of female baboons (*Papio* spp.), fecal testosterone was positively associated with dominance rank, but not aggression (Beehner, Phillips-Conroy, and Whitten 2005). In contrast, in a population of mandrills (*Mandrillus sphinx*), there was no relationship between female dominance rank and fecal testosterone (Setchell, Smith, and Knapp 2015). Such discrepancies have been documented in several other species, and more research is needed to understand how testosterone concentrations relate to dominance rank in female primates.

In addition to testosterone, the glucocorticoid cortisol has been researched for its association with dominance rank. Cortisol is a central compound of the physiological stress response, having a large and diverse set of metabolic and immunological functions. The patterning of cortisol secretion across animals of different dominance rank depends on a number of factors. Among mammals, subordinate individuals tend to have higher glucocorticoid levels relative to higher-ranking animals. This has been supported by early work in olive baboons (*Papio anubis*), indicating that high-ranking males have lower basal cortisol levels, but also higher cortisol responsiveness, than subordinate males (Sapolsky 1992). Low ranking males may exhibit elevated cortisol as a result of losing a majority of competitive interactions, and they may also suffer from reduced social support, access to nutrition, access to females, and other deficits

associated with being low in dominance. In general, access to social support and other related coping strategies are significant predictors of cortisol levels in primates.

Another major predictor of cortisol levels in primate social groups is the stability of the dominance hierarchy. In olive baboons, lower ranking males tend to have higher cortisol levels when dominance hierarchies are stable, and higher ranking males tend to have higher cortisol levels when hierarchies are unstable (e.g., when a new male enters the group) (Sapolsky 1992). Together, testosterone and cortisol play important, intersecting roles in primate dominance hierarchies and, at the same time, can impact primate health (Sapolsky 2005). Given the potential negative immunological properties of both hormones (McEwen et al. 1997; Muehlenbein and Bribiescas 2005), an individual's health is influenced by social and ecological circumstances that manipulate concentrations of these hormones, including rank instability, reproductive opportunities, grooming opportunities, coping strategies, and food availability. Dominant males who must maintain high testosterone to aid in vigilance against threats to their status seemingly do so at a cost. For instance, dominant male chimpanzees at Ngogo (Kibale National Park, Uganda) who exhibit high fecal testosterone concentrations also have the highest intestinal parasite burden (Muehlenbein and Watts 2010). Likewise, subordinate animals, who face a host of the psychological stressors associated with low rank, may be impacted by high cortisol levels and may also suffer health deficits (Sapolsky 2005), such as stunted growth and suppressed immunity, as well as negative effects on reproductive outcomes (McEwen et al. 1997).

SEE ALSO: Aggression; Cortisol and Other Glucocorticoids; Female Reproductive Endocrinology; HPA Axis; Male Reproductive Endocrinology

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