

Commentary

## A continuing saga: The role of testosterone in aggression

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There can be few topics that have attracted more debate and spread such confusion than the role of testosterone in vertebrate aggression. This is due in large part to the lack of consensus on testosterone treatment and expression of aggression, but also because social interactions increase testosterone secretion in some species but not others (e.g., Harding, 1983; Wingfield et al., 1994). There have been numerous attempts to define aggression, not surprisingly given the tremendous diversity of vertebrates and the enormous variety of contexts in which aggression is expressed. For example, songbirds may use a broad spectrum of behavioral traits when expressing aggression. These include song rate, song stereotypy, number of points (with wing droops and elevated tail), trill vocalizations and wing waves, flights (around the intruder), grass/substrate pulling, bill wipes, closest approach to intruder, attacks, fights, and persistence of aggression after removal of an intruder (Sperry et al., 2003; Wingfield, 1985). Many of these traits involve a mixture of auditory and postural signals utilizing very different neuronal circuits. Additional sensory modalities may be used in other vertebrates adding greatly to the complexity of signals and neuronal circuits involved. For example, compare the hormone mechanisms underlying neural circuits for song in birds (Brenowitz, 1997) with auditory signaling in midshipman fish *Porichthys notatus* (Bass, 1996) or electrical signaling in weakly electric fish (Zakon and Smith, 2002) or social signaling in amphibians (Wilczynski et al., 1993). Note also that aggression can be expressed offensively and defensively (e.g., Brain, 1979) adding further complexity.

Despite this complexity, it has long been known that testosterone regulates territorial aggression in many

vertebrates, at least in reproductive contexts (e.g., Balthazart, 1983; Harding, 1983). For example, testosterone regulates expression of territorial aggression during ontogeny, during the development of the reproductive system, in mate-guarding aggression, and in dominance–subordination relationships in reproductively active birds (Balthazart, 1983; Wingfield and Ramenofsky, 1985). Nonetheless, the correlation of circulating levels of testosterone with aggressive behavior has been equivocal at best. Moreover, aggressive interactions among males increase testosterone in some species but not others. The result is much confusion over whether testosterone generally activates aggression at all, and in those species in which this appears to be true, why do some show social modulation of testosterone secretion and others do not? The degree to which males show such facultative increases in testosterone secretion when challenged, or in other social situations, tends to be related to mating system (Hirschenhauser et al., 2003; Wingfield et al., 1990). This generalization has been shown from fish (Oliveira, 1998) to mammals (Goymann et al., 2003; Woodroffe et al., 1997) including primates (Cavigelli and Pereira, 2000; Ostner et al., 2002). Even here there are some exceptions such as dwarf mongooses, *Helogale parvula* (Creel et al., 1993). Exceptions aside, one question that is repeatedly asked is “in those species that show social modulation of testosterone, what is the role of increased secretion of testosterone following a social interaction?” This is particularly pertinent because in virtually all cases testosterone levels increase AFTER expression of aggression in response to an intruder.

In this issue an excellent paper by Oyegbile and Marler (2005) indicates that prior winning experience in male California mice, *Peromyscus californicus*, increased the likelihood that individuals will win future fights. Furthermore, winning encounters with other males increased

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testosterone levels in plasma providing a novel association of the winner effect (repeated winning experiences) and increased testosterone levels. These data suggest a role for increased testosterone secretion following an aggressive encounter. Oliveira et al. (1998) showed that male Siamese fighting fish, *Betta splendens*, appear to monitor aggressive interactions among neighbors. Information on relative fighting ability may then be used in future aggressive interactions with those individuals. Whether testosterone facilitates this is, as far as I am aware, unknown. In song sparrows, *Melospiza melodia*, staged simulated territorial intrusions in free-living males resulted in an increase in circulating testosterone within 10–30 min (Wingfield, 1985). This and other studies such as work on captive Japanese quail, *Coturnix japonica* (Ramenofsky, 1984), and a key paper on hormone responses to aggressive interactions in natural populations of red-winged blackbirds, *Agelaius phoeniceus* (Harding and Follett, 1979), led to the challenge hypothesis (Wingfield et al., 1990). This hypothesis attempted to reconcile the tremendous variation and contradiction on testosterone and aggression in the literature by suggesting that the two were only correlated during social instability or when an individual is challenged by a conspecific. Wingfield et al. (1990) also suggested that the role of testosterone that increases after the aggressive encounter has begun is related to expression of high levels of aggression for a prolonged period especially if the intruder is persistent. Such a hypothesis is consistent with earlier results of Andrew (1972) and Andrew and Rogers (1972) showing an effect of testosterone on persistence in domestic fowl chicks, *Gallus domesticus*, in open field situations.

The idea of “persistence of aggression” being a possible role of increased testosterone secretion following social interactions was tested further in free-living song sparrows. Males with elevated testosterone after a staged territorial encounter continued to spontaneously sing, patrol the territory and attack other birds for 24 h after the stimulus had been removed (Wingfield, 1994a; Wingfield and Hahn, 1994). We interpreted this as the experimental male (staged winner) actually reinforcing his territorial status and broadcasting to other males that he was still in control. When we did the same experiment in autumn, when testosterone levels are not detectable, males still respond to territorial intrusion in a manner similar to birds in spring (Wingfield and Hahn, 1994). Even castration did not abolish this response (Wingfield, 1994a,b). However, testosterone levels did not increase in response to intrusion in autumn, and when the stimulus was removed males stopped singing and patrolling within minutes. We then gave testosterone implants to males in autumn and showed that the persistence of aggression following removal of the stimulus, and the reinforcing behavior broadcasting successful defeat of the intruder and retained territorial status, was restored (Wingfield, 1994a,b). These data clearly indicate a role for increased testosterone levels following social stimulation.

Next, it will be important to determine whether the action of testosterone on persistence of aggression is mediated by androgen or estrogen receptor pathways.

In this issue, Oyegbile and Marler (2005) point out that the mechanisms of action of testosterone in these contexts will likely include interactions with central paracrine secretions such as arginine vasopressin (AVP, or vasotocin, AVT), vasoactive intestinal peptide (VIP), dopamine, and serotonin (5-HT) all known to modulate aggressive behavior (e.g., Delville et al., 1996; Ferris et al., 1997; Goodson, 1998a,b; Viglietti-Panzica et al., 2001). Given the broad contexts of aggression and diverse vertebrate taxa, in the future we may be able to explore in much greater detail the evolution of hormonal control systems in aggressive signaling. It is likely that other roles for elevated testosterone levels following social interactions will be discovered. Finally, another important question is “through what neural pathways do social signals affect the hypothalamo–pituitary–gonad axis and secretion of testosterone?” A broad comparative approach will likely reveal exciting new concepts in the future.

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