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Testosterone and Aggression in Birds

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The familiar spring sound of birdsongs heralds the onset of territory formation and a complex sequence of interrelated events that make up the breeding period. Such songs are an integral part of the repertoire of aggressive behaviors that males use to advertise and defend territorial boundaries and to attract mates (Fig. 1). It is well established that hormones, particularly testosterone, have stimulatory effects on aggression in reproductive contexts. The prevailing "challenge" hypothesis asserts that testosterone and aggression correlate only during periods of heightened interactions between males. Under more stable social conditions, according to the hypothesis, relationships among males are maintained by other factors such as social inertia, individual recognition of status, and territorial boundaries, and testosterone levels remain low. Recent research has suggested ways in which the hypothesis should be modified or extended. In this article we will consider the complexities of aggressive behaviors and their regulation, focusing specifically on species differences in territorial behavior of male birds as models for the multiple interactions of hormones, environment, and behavior.

The secretion of testosterone by interstitial cells in the testis is controlled primarily by a glycoprotein, luteinizing hormone, secreted from the anterior pituitary gland (Fig. 2). Testosterone stimulates the development of secondary sex characteristics such as wattles, combs, spurs, the cloacal protuberance (a copulatory organ), and

in some species bright-colored skin and nuptial plumage. These characteristics are used extensively in sexual and aggressive displays (Witschi 1961).

Testosterone is also transported in the blood to the brain, where it influences the expression of reproductive behaviors. Classical experiments conducted on a variety of vertebrates, including birds, showed that if the testes are removed, there is a decline in the frequency and intensity of aggressive and sexual behaviors such as singing (or equivalent vocalizations), threat postures, and actual fights. If exogenous testosterone is given to these castrates, the frequency of aggressive behaviors

increases again (for reviews on birds see Harding 1981; Balthazart 1983).

The extent to which aggressive behaviors decline after castration or increase after administration of exogenous testosterone varies greatly from species to species, in part because of the different ways in which testosterone can influence behavior.

Two mechanisms have been proposed involving organizational and activational effects. Organizational effects of testosterone occur early in development, often immediately after hatching, and once adulthood is reached the neurons involved can operate independently. Activational effects require the immediate presence of testosterone for the sensitive neurons to function normally. Whether organizational or activational effects predominate depends on context and stage in the breeding period. However, in birds it appears that testosterone may have important activational effects regulating short-term changes in territorial aggression within the breeding season.

Over the past 15 years, radioimmunoassay has been used to determine circulating levels of testosterone. If testosterone does activate aggressive behavior, plasma levels should correlate with the behavior in reproductive contexts. Recent work on rodents (Schoorman 1980; Brain 1983; Sachser and Pröve 1984) and primates (Eaton and Resko 1974; Dixson 1980; Phoenix 1980; Bernstein et al. 1983; Sapolsky 1984) suggests that there are such correlations, but that they depend to a great extent on taxonomic class, age, experience, social context, and other environmental influences. The mechanisms underlying such variation are still largely unknown.

In birds, the evidence for correlations of testosterone and aggression is more convincing, although not completely so. Once again, social context must be taken

*Testosterone may not
trigger aggressive
behavior but may facilitate
responses to it*

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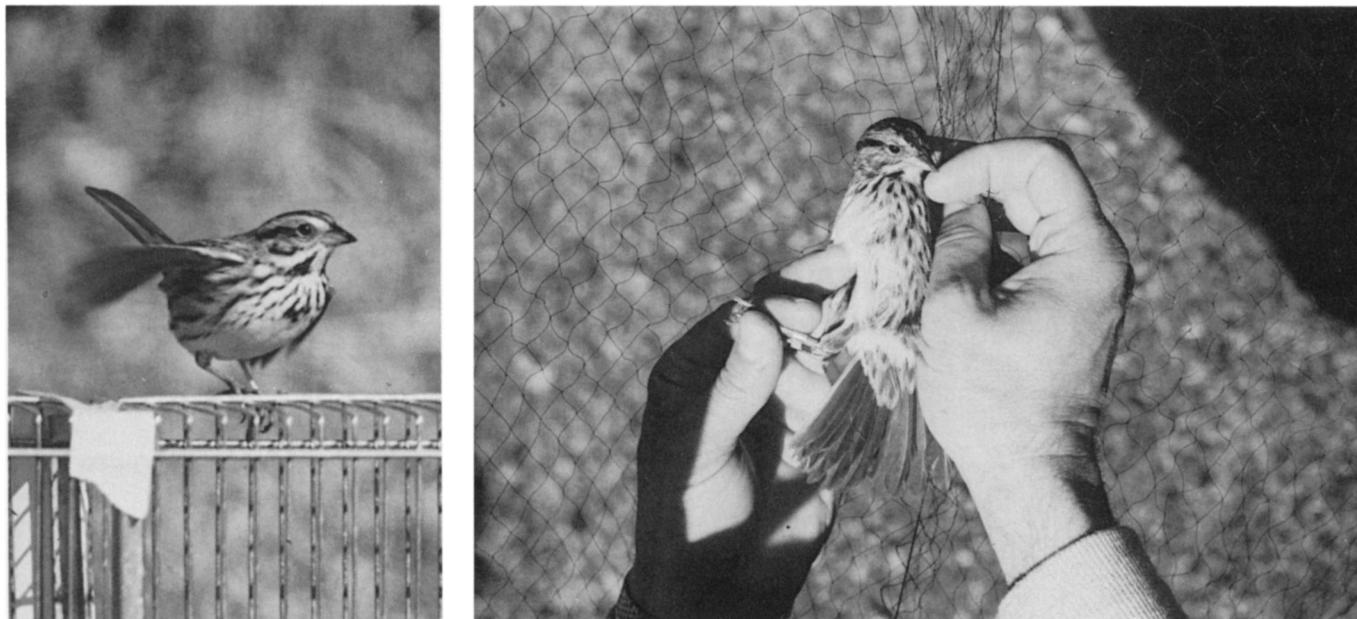


Figure 1. As part of the annual ritual of establishing territories and attracting mates, male birds engage in a variety of aggressive behaviors. In the photograph on the left, a male song sparrow (*Melospiza melodia*) assumes the posture that heralds an attack on an intruder, in this case a decoy in a cage. Recent research has shown how the steroid hormone testosterone stimulates aggression in response to such perceived threats. Mist nets stretched between aluminum poles are used to catch birds in the field. After removing a bird from the net (right), the scientist collects a blood sample from a wing vein. The bird is then released unharmed. (Photographs by J. C. Wingfield.)

into account, as well as environmental influences such as length of day, presence of a mate, and nest sites (Wingfield and Ramenofsky 1985). At least some of this confusion can be eliminated by bringing a comparative approach to bear on a variety of avian species. Birds are ideal for this kind of research because there is much diversity in social systems across species. They are also relatively easy to study under free-living conditions, enabling us to conduct parallel field and laboratory investigations.

Seasonal changes

If testosterone is as intimately involved with territorial aggression in birds as is usually presumed, testosterone levels in the blood should parallel the expression of seasonal territoriality. This relationship has been investigated in several species of birds under free-living conditions, thus reducing possible artifacts of captivity (see Wingfield and Farmer 1976).

It is crucial when analyzing these kinds of data to determine the precise stage in the reproductive period at which each individual is sampled. This point is illustrated in Figure 3, which depicts plasma levels of luteinizing hormone and testosterone in free-living house sparrows (*Passer domesticus*). If plasma levels of a number of individuals are organized by calendar date, several stages of reproductive activity (prelaying, laying, incubating, reneating) are averaged out on any given date, and the result is a pair of curves, with luteinizing hormone and testosterone rising in spring, remaining relatively high during the breeding season, and then declining to basal as reproduction ends in August and September. If the data are reorganized according to the phase of the breeding cycle, the true pattern of hormone variation is revealed, making allowance for the average

time it takes a pair to progress through each stage (about 4 to 6 days to lay the first egg, 5 days to produce a clutch, and 11 to 14 days to incubate).

Figure 4 compares levels of testosterone in several monogamous species sampled in free-living conditions. Typically, testosterone is highest when territories are first established and aggressive interactions among males are most frequent. For the song sparrow (*Melospiza melodia*), there are two peaks of testosterone, the first associated with the establishment of territory and the second with the egg-laying period for the first clutch, when the male guards his sexually receptive mate. Plasma levels of testosterone decline markedly just prior to or during the parental phase (incubation) and gradually diminish to basal concentrations by the end of the breeding season.

There is no increase in plasma levels of testosterone during the egg-laying period of the second brood for many of the species with open-cup nests, such as the song sparrow and the European blackbird (*Turdus merula*), because there are virtually unlimited sites for these nests, and competition focuses on maintaining territorial boundaries and guarding mates. However, species such as the house sparrow and the European starling (*Sturnus vulgaris*) that nest in holes, a limited resource for which there often is intense competition (in addition to guarding mates), do show an increase in testosterone level with each egg-laying period (see Figs. 3 and 4).

An interesting contrast is provided by the western gull (*Larus occidentalis wymani*). Individuals of this species are long-lived, may breed for 20 years or more, usually mate for life, and return to the same breeding territory year after year. Furthermore, there is an excess of females and no shortage of nest sites at one of the breeding colonies, Santa Barbara Island (Hunt et al. 1980). As a result, competition between males is mini-

mal, and it is not surprising, given the low level of aggression, that the cycle of plasma testosterone in male western gulls is of very low amplitude (Wingfield et al. 1982).

As Figure 5 shows, the same relationship of testosterone levels and aggression can be found in polygamous and promiscuous species, but males of these species have high levels of testosterone for longer periods than do monogamous species. For example, male red-winged blackbirds (*Agelaius phoeniceus*) generally do not feed young but rather display at one another throughout the breeding season in an attempt to maintain territorial boundaries and retain females.

Both monogamous and polygynous males are found within populations of the pied flycatcher (*Ficedula hypoleuca*). Monogamous males have testosterone levels similar to those of monogamous males in other species, but polygynous males maintain high levels of testosterone until the second female has begun incubating. Only then do levels decline rapidly, followed by a return of the male to his first mate, whose young he helps to feed (see Silverin and Wingfield 1982).

Male brown-headed cowbirds (*Molothrus ater*) are unusual in that they do not defend a territory but form dominance hierarchies for access to females. They are brood parasites, showing no parental care. Males spend the entire breeding season guarding females from the attentions of other males. Accordingly, we see prolonged high levels of testosterone that decline only gradually during the season (Dufty and Wingfield 1986a).

Laboratory tests of the challenge hypothesis

As we have seen, field investigations of free-living birds suggest that testosterone is elevated during periods of elevated competition between males, and that parental behavior in males is preceded by a decline in testosterone. Only in species in which males do not feed young or are exposed to intense competition do plasma levels of testosterone remain elevated. These results have led to the challenge hypothesis.

What is the experimental evidence in support of the hypothesis? A positive correlation of aggressive displays with plasma testosterone was found when Japanese quail (*Coturnix coturnix*) were paired in a tournament lasting several days, but the correlation was apparent only immediately prior to the first fighting day and during the following three days (Ramenofsky 1984). From the fifth day onward, levels of testosterone in quail that won fights were indistinguishable from levels in those that lost. By that time, dominance relationships had been established. This may explain why Balthazart and his colleagues (1979) and Tsutsui and Ishii (1981) could find no correlation of plasma testosterone level

and dominance status in groups of male quail with well-established social relationships.

Other experiments confirmed these findings. Captive flocks of house sparrows formed social hierarchies in which dominant individuals had higher plasma levels of testosterone than subordinates only during the first week after the birds were grouped. Before grouping, and more than one week after, there were no correlations of

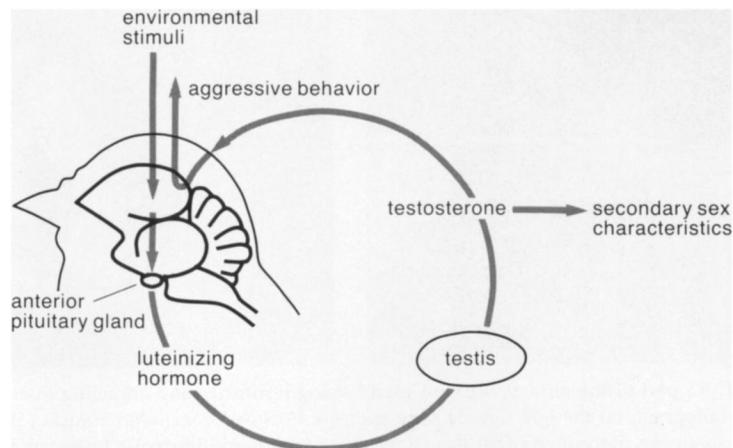


Figure 2. The system through which testosterone influences aggressive behavior begins with the secretion, in response to environmental stimuli, of the glycoprotein luteinizing hormone from the anterior pituitary gland at the base of the brain. Luteinizing hormone in turn stimulates secretion of testosterone by interstitial cells in the testis, where testosterone is produced. In addition to arousing aggressive behavior, testosterone contributes to the development of secondary sex characteristics, such as combs, spurs, and bright plumage.

testosterone level and social status (Hegner and Wingfield 1986). This is consistent with the challenge hypothesis, since testosterone levels were elevated only for a short period as relationships were established. Similarly in the brown-headed cowbird, three males grouped with a single female formed social relationships, and the dominant male gained access to the female. Plasma levels of testosterone in dominant males were elevated one day after grouping, but not before or one week after (Dufty and Wingfield 1986b).

What happens if exogenous testosterone is given to individuals? Do they rise in status, gain a territory, or enlarge an existing one? If a testosterone implant was given to an identified subordinate of a regularly matched pair of Japanese quail, he became more aggressive and fought more persistently with other males. Nevertheless, these subordinates did not win a sufficient number of fights to be considered dominant (Ramenofsky 1982). This suggests that testosterone is not sufficient in itself to heighten aggressive displays to the point of overthrowing previously established relationships. Similar results have been obtained in dominance hierarchies of California quail (*Lophortyx californica*), free-living Harris's sparrows (*Zonotrichia querula*), and sharp-tailed grouse (*Tympanuchus phasianellus*) (Emlen and Lorenz 1942; Trobec and Oring 1972; Rohwer and Rohwer 1978).

Another laboratory experiment sheds more light on the challenge hypothesis. Castrated male white-crowned sparrows (*Zonotrichia leucophrys gambelii*) were given implants of testosterone that maintained circulating levels very similar to those observed during the spring (see Wingfield and Farner 1978a, 1978b). Castrated controls

were given empty implants. Songs and threat displays often seen during the establishment of territories in the field increased in both groups after treatment, but there was no significant difference in the frequency of these actions between the two groups despite the wide difference in testosterone level (Wingfield 1985a).

This apparent contradiction of the challenge hypothesis can perhaps be attributed to the fact that the birds had been housed together for over six months. It was thus likely that social relationships among individuals had been established for some time. When a new male was introduced in an adjacent cage, there was an immediate increase in aggression in both groups, and the males with higher levels of testosterone showed significantly more aggressive displays than did the controls. By the next day, the frequency of aggression had dropped dramatically, illustrating how quickly social relationships can be established and emphasizing the ephemeral nature of the correlation between testosterone and aggressive behavior.

It is of little surprise that some investigations have identified hormone-behavior relationships and some have not, particularly since social contexts vary across the studies. Experiential factors such as the development of dominance relationships among individuals can exert a strong influence on the degree to which the circulating levels of testosterone affect frequency and intensity of aggressive behavior. Nevertheless, there is little doubt that testosterone is requisite for increased frequency of aggressive behavior when an individual is challenged in a territorial or other reproductive context.

Environmental cues and testosterone

What controls the timing and amplitude of changes in plasma levels of testosterone so that they occur at appropriate stages in the reproductive period? Clearly, environmental cues play a major role, and one obvious candidate is the annual change in the length of day. It is well known that the vernal increase in length of day promotes secretion of luteinizing hormone and steroid hormones such as testosterone (e.g., Farner and Follett 1979; Wingfield and Farner 1980). Experiments with male white-crowned and song sparrows demonstrated that spermatogenesis is completed, secondary sex characteristics are developed, and the full repertoire of reproductive behaviors (both territorial and sexual) are expressed when birds are transferred from short to long days (see Wingfield and Moore 1986). However, the seasonal changes in testosterone in free-living males are dramatically different from those generated solely by exposing captive males to long days in the laboratory, and the absolute levels can reach an order of magnitude higher than those of males maintained in captivity. Since it has also been shown that high circulating levels of testosterone are not required for the expression of sexual behavior (Moore and Kranz 1983), it is possible that elevated levels in free-living males are involved solely in the regulation of aggression.

What other environmental cues influence the secretion of testosterone and aggressive behavior? Two possibilities spring to mind: stimuli from the territory itself or signals emanating from a challenging male. To evaluate these possibilities, male song sparrows were captured

and removed from their territories, thus creating a vacant spot within the local population. Usually another male claimed the spot within 12 to 72 hours. The result was an increase in conflict between the replacement male and the neighbors, who reestablished territorial boundaries with the newcomer. During this period of social instability, blood samples were collected from replacement males and neighbors. Samples were also

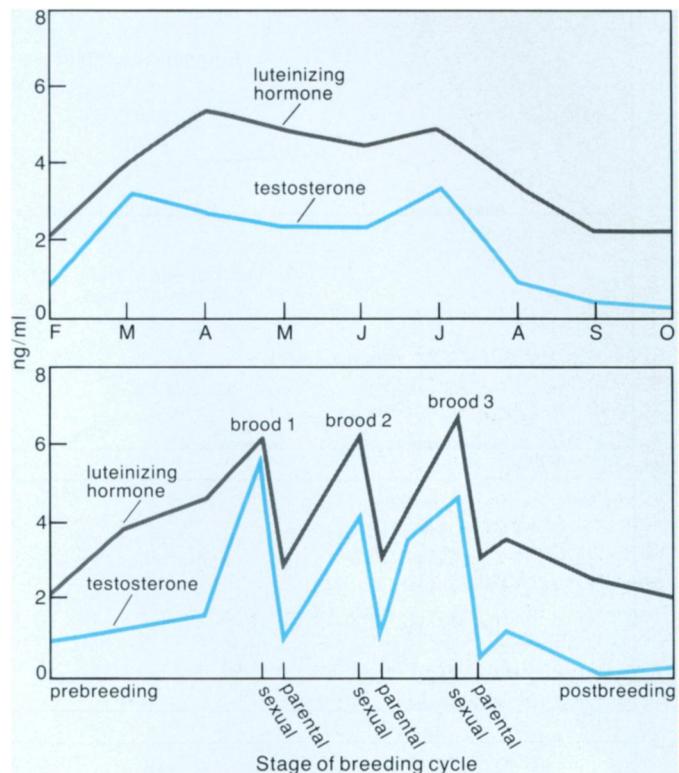


Figure 3. It is important when analyzing seasonal changes in luteinizing hormone and testosterone to distinguish between organization of data by calendar date and by stage in the breeding cycle. If plasma levels of a number of individuals are organized by calendar date (*top*), the various stages in the breeding cycle average out, and the result for both luteinizing hormone and testosterone is a curve with two peaks. If on the other hand the data are organized by stages in the breeding cycle (*bottom*), a much more complicated pattern of hormone variation appears. The data displayed here are from free-living male house sparrows (*Passer domesticus*). (After Hegner and Wingfield 1986.)

collected from control males in a separate area in which boundaries had been stable for some time.

The results were quite clear: plasma levels of testosterone were higher in the replacement males and in their otherwise untreated neighbors than in the controls. Both the neighbors of the replacement and the controls had territories, yet the latter had much lower levels of testosterone. These two groups differed only in that the neighbors were reestablishing territorial boundaries whereas the controls were not. This suggests that the stimulus for increased secretion of testosterone may be not the territory per se (although the data do not disprove a possible effect) but the challenging behavior of the replacement male as he attempts to establish new territorial boundaries (Wingfield 1985b).

To test this further, intrusions were simulated with a decoy male song sparrow in a cage placed in the center

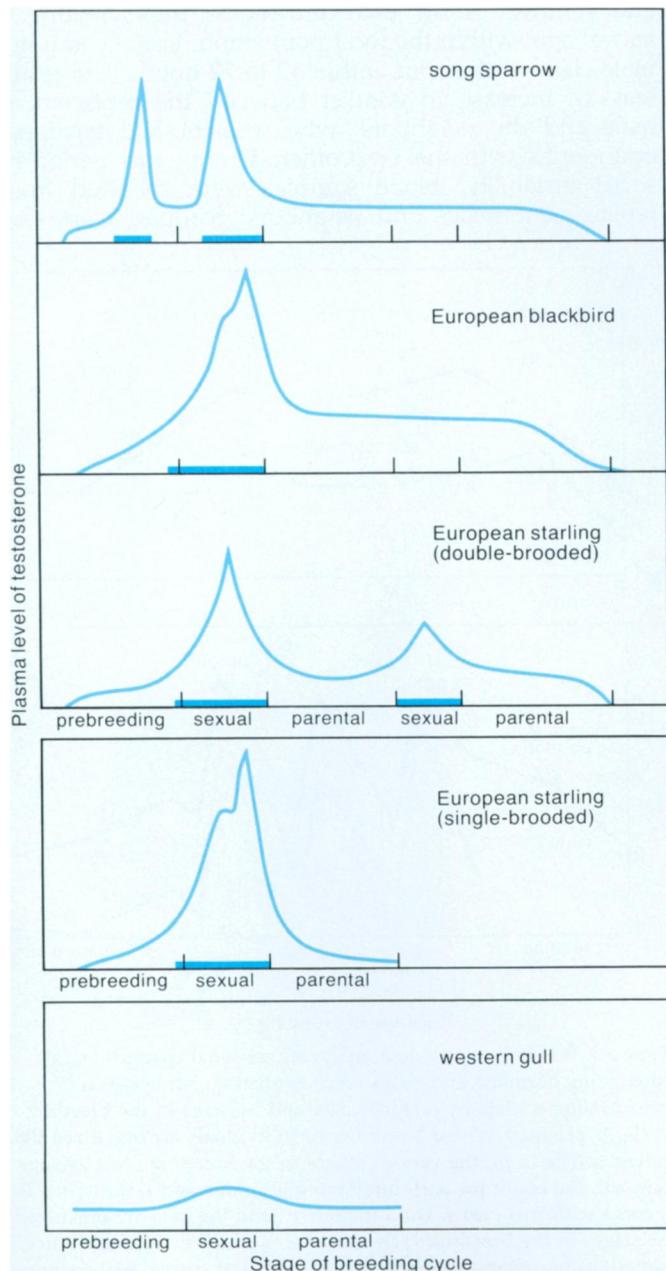


Figure 4. The plasma levels of testosterone in males of four other monogamous species are quite different from those of the house sparrow shown in Figure 3, although in all cases a relationship between testosterone and aggressive behavior is discernible. (Periods when confrontations between males are most frequent are indicated by bars.) There are two peaks for the song sparrow (*Melospiza melodia*), the first associated with the establishment of territory and the second with the egg-laying period of the first brood. The European blackbird (*Turdus merula*) has a single peak during the first brood. Neither the song sparrow nor the European blackbird has a peak during subsequent broods, because these species nest in open cups, for which there are unlimited sites and thus little competition. In these species, competition between males is most intense early in the season. The European starling (*Sturnus vulgaris*), on the other hand, nests in holes, for which competition is keen, and so starlings with double broods have a second peak during their second brood; those with single broods have the expected single peak. The western gull (*Larus occidentalis wymani*) has a distinctively different pattern because of the relative lack of conflict in its breeding colonies. (After Schwabl et al. 1980; Wingfield et al. 1982; Dawson 1983; Wingfield 1984a; Ball and Wingfield 1986.)

of a territory (see Fig. 1). Tape-recorded songs also were broadcast through a speaker placed alongside the decoy. The territorial male almost invariably attacked and attempted to drive the simulated intruder away. He was captured after skirmishing with the intruder for 5 to 60 minutes, and a blood sample was drawn. Controls were captured at the same time of day as the simulated intrusions. Males exposed to a challenge from a simulated intruder showed an increase in testosterone compared with controls. Essentially the same result was obtained in early April and in May through June, indicating that this effect could occur at any time during the breeding period.

It is important to note that the response required about ten minutes before the increase in testosterone was significant. We know that males tend to trespass on other territories regularly and are quickly chased out when seen by the owner (Wingfield 1984b). The confrontations usually last only a few seconds, and thus an increase in testosterone level is unnecessary. However, if an intruder persists and attempts to take over the territory, prolonged fights lasting several hours or even days may result. In such cases an increase in plasma testosterone is appropriate.

There is a third line of evidence suggesting that encounters between males can result in an increase in plasma levels of testosterone. Implants of testosterone in free-living male song sparrows resulted in heightened aggression for longer periods than in control males. In turn, plasma levels of testosterone were elevated in neighbors of testosterone-implanted males compared with neighbors of controls. This effect was most apparent early and late in the season. At other times no effect was noted, because factors such as the presence of young possibly overrode the effect of the aggressive male neighbor.

It was also found that males who had a territory at least one removed from a testosterone-implanted male did not have elevated levels, even though they could hear and see encounters between their immediate neighbors and the testosterone-implanted males (Wingfield 1984b). It appears that an individual male must be involved directly in an agonistic encounter for a hormonal response to be initiated. This blocking of a ripple effect may be adaptive; otherwise, a wave of responses would pass indiscriminately through the local population, affecting males that were not involved in the original skirmish. Moreover, functionally irrelevant surges of testosterone could interfere severely with other reproductive activities such as the feeding of young.

The environmental stimuli generated in the course of an agonistic encounter could enter the central nervous system by several routes: visual, auditory (songs and other vocalizations), tactile (fights), or chemical (pheromones). We can rule out tactile stimuli, because several of the experiments outlined above show that testosterone levels increase in response to a caged male with whom contact is precluded. Also we can probably rule out pheromonal cues, since these are largely regarded as being absent in birds (although it is important to note that this point has not been rigorously investigated). Thus we are left with visual and auditory information influencing secretion of testosterone.

Are both components required for the response?

Recent field experiments showed that if male song sparrows are exposed to a playback of tape-recorded songs (auditory but no visual stimulus), a devocalized male (visual but no auditory stimulus), or a playback plus a devocalized male (visual and auditory stimuli), only those males exposed to both visual and auditory cues have elevated levels of testosterone. Auditory or visual cues alone do not result in a significant increase in testosterone. It was also found that the response is specific: captive male song sparrows showed an increase in plasma levels of testosterone following a challenge from another song sparrow but not following a challenge from a house sparrow (a heterospecific).

Now that the external receptors for environmental cues have been identified and the endocrine response and the specificity of that response determined, we can investigate the neural pathways by which environmental information controls reproductive function.

What is testosterone doing?

This may appear to be an odd question, since it is well established that testosterone has direct effects on aggressive territorial behavior. There is no doubt that testosterone has organizational effects insofar as it influences the formation of song control nuclei in the brain during development and seasonal breeding (e.g., Nottebohm 1981). It is also clear that high levels of testosterone during establishment of a territory are playing some activational role, at least early in the breeding season. However, many of our observations do not fit neatly into these categories (see also Arnold and Breedlove 1985).

Responses to challenges outside the normal seasonal pattern suggest another role for testosterone in the arousal of aggressive behavior. The initial response to a challenging male is to attack vigorously even though the circulating level of testosterone may be much lower than in early spring. Only *after* the attack does testosterone increase, and this appears to take at least ten minutes. Clearly testosterone cannot be playing an activational role in the literal sense of the word, since it increases after the fact. Is it possible that testosterone is playing a facilitative role for the neurons involved during extended periods of intense aggression?

This role would require a very rapid action of a steroid hormone on a target cell. The classical mode of action is through the genome, a process that can take many hours (typically 16 to 30). But recently compiled evidence from mammals suggests that steroid hormones can also have very rapid effects. For example, steroids have been shown to influence rates of gene transcription in rats within 15 minutes, and estradiol can have morphological effects on neuronal cell nuclei within two hours (Jones et al. 1985; McEwen and Pfaff 1985). Even more striking is the demonstration *in vitro* that estradiol injected directly onto the membrane of an excitable cell induces action potentials within one minute (Duffy et al. 1979). Furthermore, Towle and Sze (1983) found that several steroid hormones, including testosterone, bind to synaptic membranes in the rat brain with high specificity and affinity. Thus the potential exists for very rapid actions of testosterone on the central nervous system through membrane receptors, although more research is required to confirm this in avian systems.

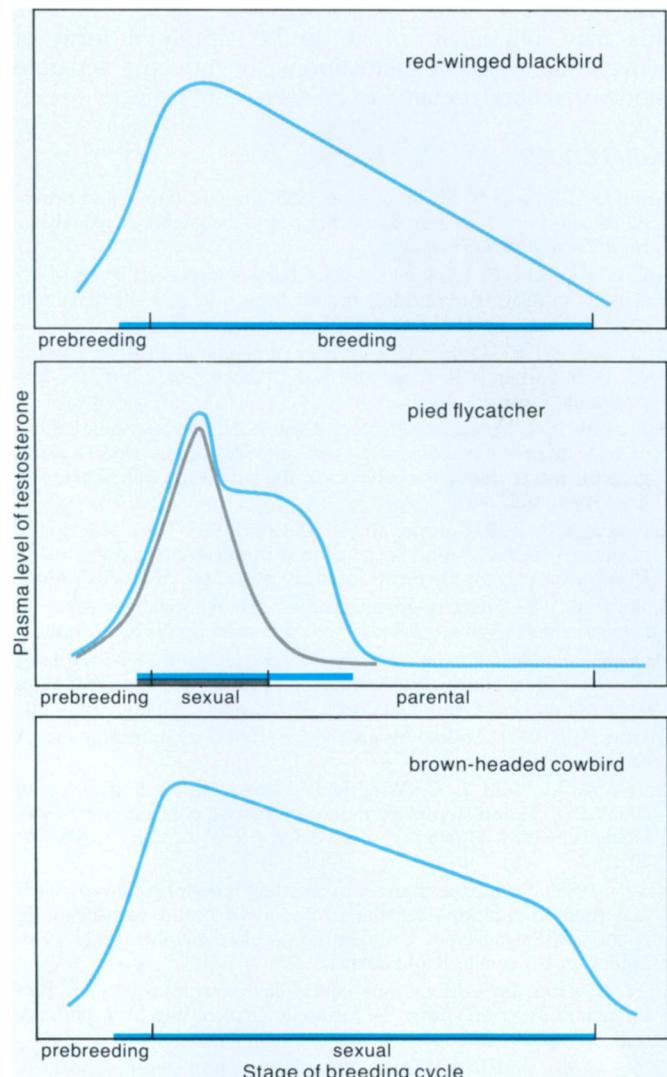


Figure 5. Males of polygynous and promiscuous species have their own characteristic patterns of circulating testosterone: levels remain high for longer periods than they do in monogamous species (see Fig. 4). These correlate with the greater amount of time that such males must spend defending territories and females. (Periods of frequent conflicts between males are again indicated by bars.) In red-winged blackbirds (*Agelaius phoeniceus*), the breeding period includes both sexual and parental stages, since each male may have several females on his territory, some of which may be in the sexual or parental stage at any one time. The pied flycatcher (*Ficedula hypoleuca*) includes both monogamous (gray line and bar) and polygynous males (colored line and bar). The brown-headed cowbird (*Molothrus ater*) is a brood parasite that has no territory and performs no parental duties but rather spends the breeding season guarding females from competing males. (After Silverin and Wingfield 1982; Duffy and Wingfield 1986a. Additional data supplied by W. A. Searcy.)

Such a concept is speculative, but the possibility arises that in addition to the two classical modes of genomic action of steroid hormones, involving organizational and activational effects, a third mode of action—supporting or facilitative—could arise during periods of heightened agonistic encounters. Mediated either through rapid-acting membrane receptors or genomically, the third mode would influence the function of brain nuclei involved in the control of aggression. Whether

this may ultimately prove to be simply a form of activational effects of testosterone, or indeed a separate mode of action, remains to be seen.

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