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John C. Wingfield; Robert E. Hegner; Alfred M. Dufty, Jr.; Gregory F. Ball

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THE "CHALLENGE HYPOTHESIS": THEORETICAL IMPLICATIONS FOR PATTERNS OF TESTOSTERONE SECRETION, MATING SYSTEMS, AND BREEDING STRATEGIES

JOHN C. WINGFIELD, ROBERT E. HEGNER, ALFRED M. DUFFY, JR.,
AND GREGORY F. BALL

Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195; 7629 Matera
(101), Falls Church, Virginia 22043; Department of Biology, 1910 University Drive, Boise State
University, Boise, Idaho 83725; Department of Psychology, 502 McGuinn Hall,
Boston College, Chestnut Hill, Massachusetts 02167

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A number of investigations in recent years have shown that seasonal profiles of testosterone (T) levels in the blood of male birds breeding under natural conditions are highly variable. As a result of the application of field endocrinology techniques (see Wingfield and Farner 1976), the temporal patterns of T secretion in free-living males are now known for over 20 species (from 6 orders and 14 families), representing three mating systems (monogamy, polygyny, and polyandry) and several breeding strategies. Results of these studies provide the impetus for an assessment of the potential relationships between T and breeding systems. The concepts emerging from their analysis can serve both as a framework for further investigation of the hormonal mechanisms underlying social behavior of vertebrates in general and as a guide for manipulating social systems to gain new insights into the ultimate cause of different mating strategies. The extent of these differences varies considerably among species (Wingfield 1984a; Wingfield et al. 1987) and raises a number of questions. Why is there so much variation in the temporal patterns of circulating T levels between captive and free-living populations and among species? Are there relationships between temporal patterns of T secretion and mating systems or the breeding strategies of individuals? What are the environmental and genetic determinants of these patterns and their functions?

In this article we consider some theoretical approaches to the interrelationships of T, mating system, and breeding strategy in male birds using data from captive and free-living populations. To make our assumptions explicit, we begin with a summary of the actions of T in male birds. We then address the questions above by considering the temporal patterns of T secretion and their correlations with mating systems and breeding strategies.

We have restricted this discussion and analysis mostly to the class Aves simply because there is a large data base from a wide range of mating systems and breeding strategies. It should be noted, however, that the conclusions made here may also be equally applicable to all the vertebrate classes.

BIOLOGICAL ACTIONS OF TESTOSTERONE

Extensive evidence in birds suggests that T is involved in spermatogenesis (see, e.g., Brown and Follett 1977) and in the development of at least some secondary sex characters, including vas deferens, cloacal protuberance and associated glands, combs, wattles, modified plumes, and, in some species, development of brightly colored nuptial plumage (Witschi 1961; Wingfield and Farner 1980a). T also regulates the expression of reproductive behaviors, both sexual and aggressive (review in Balthazart 1983). There is accumulating evidence that T is metabolized within target cells to estradiol or other compounds that then bind to genomic receptors and mediate their effects (see Balthazart 1983). In this article, however, we focus on the pattern of T that is *circulating*, that is, before it reaches the target cell and is metabolized to other steroid hormones. Blood is the major route for transport of the steroid hormone T, and thus circulating levels are an accurate assessment of the concentration to which target cells are exposed. Other mechanisms such as metabolism within the cell are undoubtedly important, but they are beyond the scope of this theoretical approach.

Numerous investigations have shown that captive males of temperate-zone birds exposed to long days undergo gonadal development accompanied by an increase in circulating-T levels. Under these conditions, spermatogenesis is completed, all secondary sex characters develop normally, and the full repertoire of reproductive behavior (i.e., sexual and aggressive) is expressed (reviews in Wingfield and Farner 1980a, 1980b; Wingfield and Moore 1987; Wingfield et al. 1987). However, field investigations of several species have revealed that the temporal patterns of T secretion under natural conditions can differ from those induced artificially in the laboratory (see Wingfield 1980, 1983; Wingfield and Farner 1980a, 1980b; Wingfield and Moore 1987). Furthermore, the absolute level of T circulating in free-living males is, in some cases, an order of magnitude higher than in the same species held in captivity (Wingfield and Farner 1980a, 1980b; Wingfield and Moore 1987). It is unlikely that a lower level of T in captive birds is due to the stress of captivity since plasma levels of corticosterone (often used as an indicator of stress; see Siegel 1980; Harvey et al. 1984) are also higher in free-living birds (see, e.g., Wingfield and Farner 1978a, 1978b; Wingfield 1984a, 1985a). Rather, differences in T levels probably result from the restricted access of captive males to the full repertoire of environmental (particularly social) stimuli.

Figure 1 summarizes diagrammatically the differences between breeding and nonbreeding males. A nonbreeding baseline T level (*a*) increases to a breeding-season baseline (*b*) stimulated by environmental cues, for example, day length. This level (*b*) is sufficient for spermatogenesis and the development of secondary sex characters and is also adequate for at least the expression of reproductive behavior, given the correct contexts and releasers. Furthermore, this pattern and the level of T are generated under captive conditions by exposing birds to long days or other appropriate environmental stimuli and are relatively constant (except for duration) in all species. However, the T level may increase above baseline *b* to the maximum level achieved under physiological conditions (*c*). Since

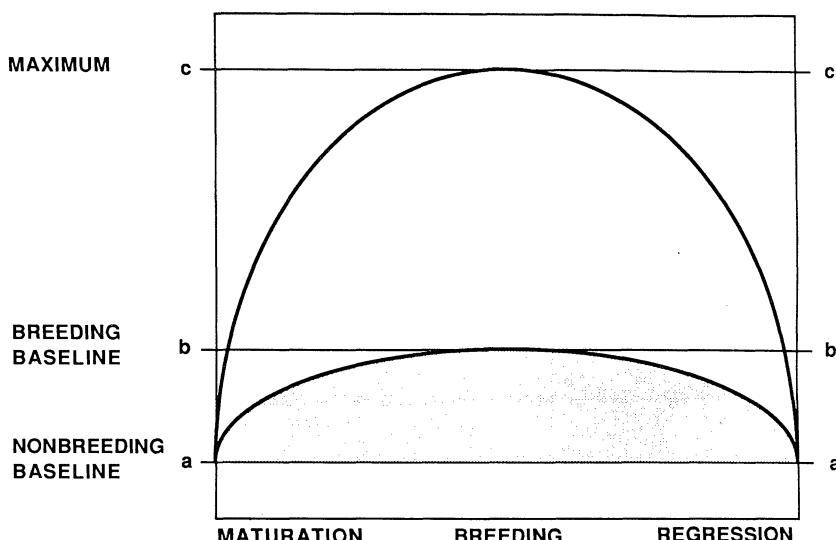


FIG. 1.—General patterns of circulating testosterone levels in male birds (ordinate) during gonadal maturation, breeding, and gonadal regression. The lower curve (shaded) represents the pattern of testosterone secretion induced by environmental cues, such as endogenous circannual rhythms and photoperiod, that is similar (except for duration) in all species. Level *a*, The non-breeding baseline of testosterone level in blood (close to zero in most species); *b*, the breeding-season baseline, often the maximum level in captive populations. Many species also have the capacity to increase the secretion of testosterone above the breeding-baseline curves in response to such environmental stimuli as male-male interactions and the presence of sexually receptive females (Wingfield 1980, 1983; see also the text). Testosterone can increase above level *b* to a maximum physiological level *c*. In contrast to the relatively stable pattern of testosterone below level *b*, the increases in testosterone above level *b* can be highly variable; they can be of short or long duration and of high or low amplitude (within the upper curve).

all cells respond to endocrine signals via receptors that are specific for each hormone, it is possible that at level *c* all central and peripheral receptors for T, or its metabolites, in all target organs would be saturated, although evidence for this is lacking. The increase in T above *b* can be short or long in duration and small or great in magnitude (varying among populations and individuals within the upper hypothetical curve in fig. 1).

Why are the absolute levels of T often much higher in the field and the patterns of T secretion (between levels *b* and *c* in fig. 1) so complex? Experimental investigations suggest that the T involved in spermatogenesis is not obtained from blood but is sequestered in the testis directly (Donham et al. 1982). Furthermore, low plasma levels of T appear to suffice for the development of secondary sex characters, suggesting that the complex patterns and higher levels in the field are not necessary for the development of gonads and accessory organs. This conception is summarized in figure 2. As T levels in the blood increase to the breeding-season baseline (*b*), the development of gonadal and accessory structures is completed. As the T level increases to the maximum (*c*), there is no further gonadal develop-

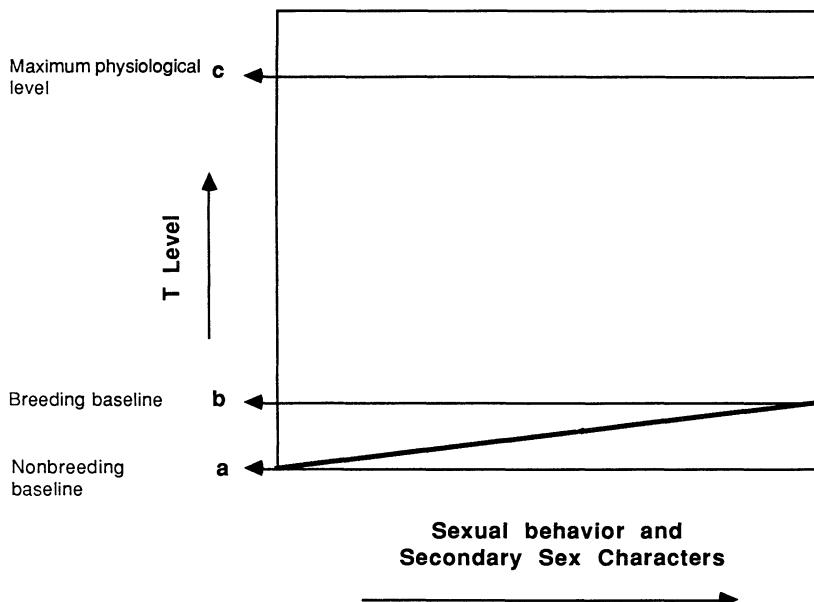


FIG. 2.—Theoretical relationships among testosterone levels (T), development of gonadal and accessory structures, and sexual behavior, including the development of secondary sex characters (based on Wingfield and Moore 1987). Testosterone levels as in fig. 1. As T levels in blood increase from *a* to *b*, the gonads, accessory structures, and sexual behavior all develop fully, with no further development as T levels increase above level *b*.

ment. Given these relationships, it is unlikely that the high concentrations and complex patterns of T above level *b* are involved in spermatogenesis and the development of secondary sex characters.

What is the relationship between circulating T and reproductive behavior? Crews (1984) and Crews and Moore (1986) have suggested that in many vertebrates high circulating levels of T and the expression of at least some sexual behaviors can be dissociated (see also Dittami and Reyer 1984). In birds, Moore and Kranz (1983) showed that castrated white-crowned sparrows (*Zonotrichia leucophrys gambelii*) mount and copulate as well as intact males, suggesting strongly that these behaviors can be expressed without high plasma levels of T (review in Wingfield and Moore 1987). In other avian species, however, levels of T at least above some minimum are required for the expression of sexual behavior (reviews in Harding 1981; Balthazart 1983). The relationship between the circulating concentration of T and sexual behavior is summarized in figure 2. As T levels increase from *a* to *b*, the expression of sexual behavior increases to a maximum; in some cases, this behavior may already be near to the maximum at level *a* (see, e.g., Moore and Kranz 1983). Any additional increase to *c* results in only a slight elevation, if any, in the frequency or intensity of sexual behavior. Although sexual behavior per se may be unaffected, there is growing evidence that the frequency and intensity of aggressive territorial and mate-guarding behavior may be modi-

fied in direct proportion to the circulating level of T. In other words, the complex patterns and high circulating levels of T between levels *b* and *c* may be involved solely in male-male aggression.

Testosterone, Aggression, and the Challenge Hypothesis

It has long been known that T increases aggressive behavior in male vertebrates. Several experiments have shown that castration tends to decrease the frequency of aggression in birds and replacement therapy with T tends to increase it (reviews in Harding 1981; Balthazart 1983). However, more-recent investigations have failed to indicate the precise nature of this relationship. It is now clear that aggression and T are not always related directly (Dittami and Reyer 1984; Wingfield and Ramenofsky 1985). In general, it appears that T is most immediately involved in aggression associated with reproduction, such as the establishment and maintenance of a breeding territory and mate-guarding behavior, rather than with other forms of aggression (e.g., anti-predator aggression, irritable aggression; see Moyer 1968; Wingfield and Marler 1988). An increase in the frequency or intensity of reproductive aggression as an effect of T is strongest in situations of social instability, such as during the formation of dominance relationships, the establishment of territorial boundaries, or challenges by a conspecific male for a territory or access to mates (e.g., in birds, Wingfield 1985a, Wingfield and Ramenofsky 1985, Wingfield et al. 1987; in reptiles, Moore 1988; in fish, Cardwell 1989; for a general review, see Wingfield and Marler 1988). Conversely, the level of aggression declines during socially stable periods and when territories have been established, with status or boundaries maintained by social inertia (Wingfield 1985a; Wingfield and Ramenofsky 1985; Wingfield et al. 1987). Thus, circulating levels of T increase during periods of heightened aggression, possibly stimulated by male-male interactions (see Wingfield 1985a), and decline during less aggressive periods, possibly as a result of decreased male-male interactions (see Wingfield et al. 1987 and below).

This relationship of T and aggression is summarized diagrammatically in the upper panel of figure 3. According to this view, there is no change or only a modest increase in aggression as T levels rise to the breeding-season baseline (*a* to *b*). If correct, this may explain some of the controversy in the literature, especially for cases in which no relationship of T and aggression has been found in captive males. As T levels increase above *b*, however, male-male aggression increases proportionately to the theoretical limit, *c*, which is thus the maximum effective level. As a result, level *c* is fixed; and beyond this upper limit (e.g., induced by the administration of exogenous hormone), T theoretically has no further action.

What kinds of stimuli elicit T secretion above the breeding-season baseline, *b*? They include interactions among males as territories are established or existing boundaries are modified, challenges from conspecific males, and the sexual behavior of conspecific females (rising T levels promote mate-guarding behavior in this instance). (For details, see Moore 1982, 1983; Wingfield et al. 1987; Wingfield 1988.) Thus, the interrelationship of T and reproductive aggression is complex. Behavioral interactions increase T levels above *b* to *c* and, in turn, elevate the

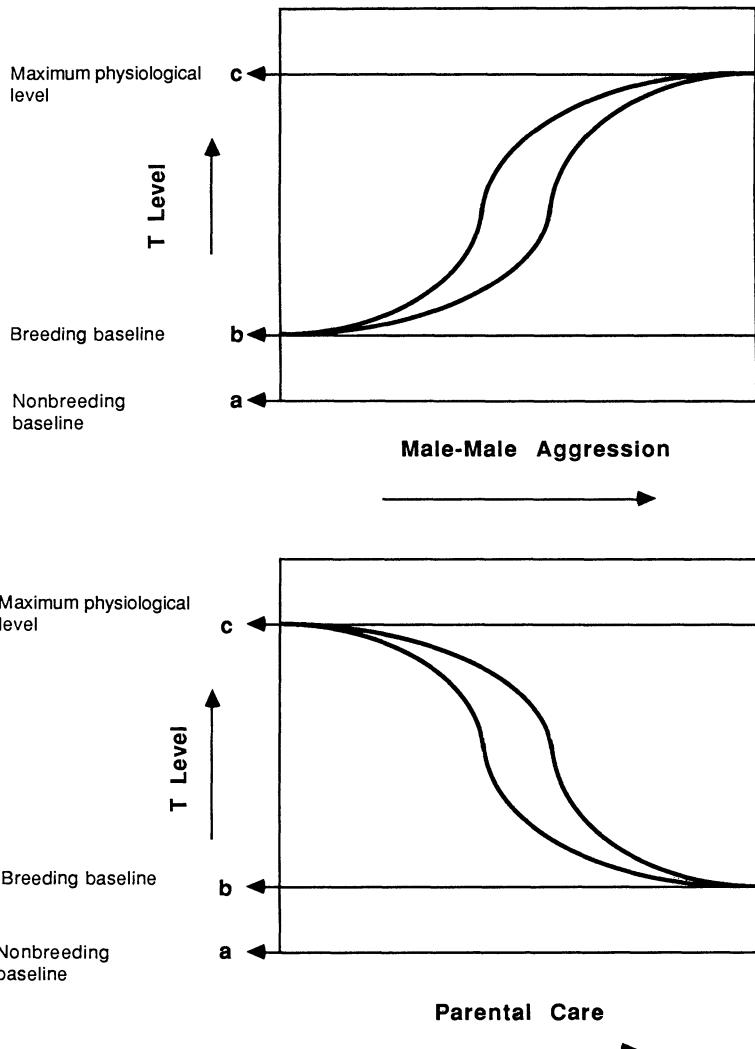


FIG. 3.—Theoretical relationship of testosterone level (T) with the frequency and intensity of male-male aggression (*upper*) and with the expression of parental (paternal) behavior (*lower*). These curves are based on published articles cited in the text. Testosterone levels as in fig. 1. As circulating T levels increase from *a* to *b*, the expression of male-male aggression does not change (i.e., the baseline levels of aggression are probably relatively independent of T). As T levels increase above *b*, there is a positive and proportional increase in male-male aggression up to a maximum at *c*. Elevation of T levels above *c* (e.g., induced by the administration of exogenous hormone) causes little or no further biological effect. In the lower panel, as circulating levels of T increase from *a* to *b*, there is no effect on the expression of parental behavior (i.e., parental behavior reaches its maximum expression and is relatively independent of T within this range of concentration). As levels of T increase above *b* to *c*, the expression of parental behavior decreases. There is little or no further suppression of parental behavior with any additional elevation (e.g., as induced by the administration of exogenous hormone) of T above *c*.

frequency and intensity of territorial and mate-guarding aggression. This apparent "positive" feedback loop remains in effect up to the maximum level, *c*, or until the source of the stimulation (behavioral interactions) is withdrawn. Once a rival male is repelled or a female is no longer receptive, the stimulation for T secretion to level *c* is removed and T concentrations drop to level *b*.

TESTOSTERONE, MATING SYSTEMS, AND BREEDING STRATEGIES

The apparent relationship between temporal patterns of T and male-male aggression gave rise to a hypothesis of correlations between T patterns and the reproductive strategies of male birds. Males of polygynous species may have higher levels of T for longer periods during the breeding season than do males of monogamous species (Wingfield 1984a; Wingfield et al. 1987). Confidence in this correlation was strengthened by the finding that if T was implanted into normally monogamous males, such that high vernal T concentrations (at level *c*) were maintained for periods longer than normal, then these males became polygynous (Wingfield 1984a). Implanted males were more aggressive and maintained territories that averaged more than twice the size of controls, thus allowing the settlement of more than one female. Since polygynous matings are likely to increase an individual male's reproductive success markedly, and since a simple increase in T appears to promote polygyny in normally monogamous birds, why do we not see more polygyny in birds? Presumably, costs of polygyny or possibly costs of maintaining high levels of T outweigh the potential increase in reproductive success.

Costs of High Testosterone Levels

It is possible that high plasma levels of T and the resulting increased activity associated with aggression expose the individual to predation, may attract predators to nest sites, and are energetically expensive. An elegant study on a lizard (*Sceloporus jarrovi*) showed clearly that experimentally induced high levels of T for long periods resulted in a marked increase in mortality (Marler and Moore 1988). However, although male song sparrows (*Melospiza melodia*) implanted with T had less fat and lower body mass than controls during the early breeding season, by the end of breeding, controls and T-implanted males were all lean (Wingfield 1984a). Furthermore, plasma levels of corticosterone (a measure of stress in birds; Siegel 1980; Harvey et al. 1984) were not different. Thus, the evidence for increased "stress" in T-implanted birds was weak. Overwintering survival rates of implanted versus control and untreated birds were also similar (Wingfield 1984a). In contrast, male brown-headed cowbirds (*Molothrus ater*) implanted with T did suffer increased mortality (Dufty 1989).

It is also possible that reproductive success is affected adversely despite polygynous associations. In many monogamous avian species, males provide substantial parental care (see Silver et al. 1985). Moreover, the experimental induction of high levels of T in males during the parental phase (above level *b* in fig. 1) suppresses parental behavior in favor of territorial aggression and mate guarding. In house sparrows (*Passer domesticus*) and pied flycatchers (*Ficedula hypoleuca*)

leuca), the suppression of parental behavior in males implanted with T resulted in a dramatic reduction in reproductive success, specifically, in reduced numbers of young per brood investigated (Silverin 1980; Hegner and Wingfield 1987).

This phenomenon is supported further by the observation that T levels rise above b during the mate-guarding period for the first clutch in multiple-brooded song sparrows and white-crowned sparrows (*Z. l. pugetensis*) but not during the mate-guarding period for the second clutch (Wingfield and Farner 1978a; Wingfield 1984b). During the egg-laying period for the second clutch, the male is feeding fledglings, and any increase in T above b at this time would inhibit parental care (level b is sufficient to maintain sexual behavior at this time). However, if first clutches or broods are lost to a predator or storm, then T levels do rise during the laying period for a second (replacement) clutch (Wingfield and Farner 1979; Wingfield 1985b). In other vertebrate classes, data on this point are scarce. However, Townsend and Moger (1987) found that plasma levels of T declined in male *Eleutherodactylus* frogs displaying parental behavior (guarding clutches of eggs).

The evidence to date suggests that as T levels increase from a to b , there is no effect on parental behavior in males (i.e., it can be expressed maximally); but as T levels increase to c , parental behavior declines proportionately. Above c (the maximum physiological level), there is no further inhibitory effect.

THEORETICAL PREDICTIONS OF TEMPORAL PATTERNS OF TESTOSTERONE IN RELATION TO MATING SYSTEMS AND BREEDING STRATEGY

The temporal pattern of T secretion above the breeding baseline, b , can be considered a trade-off between male-male aggression and parental behavior. If so, it is then possible to predict the temporal patterns of T depending on the degrees of male-male aggression and parental care expressed by males in a given population (single-brooded populations, fig. 4; double-brooded populations, fig. 5). Degrees of male-male aggression are easily subdivided into three categories: high (males interact aggressively throughout the breeding season); moderate (males interact aggressively for part of the breeding season, but the frequency of aggression abates once the parental phase is under way); and low (males interact aggressively for only a brief period at the beginning of the breeding season or show virtually no aggression at all). Parental care is less easy to categorize, but two levels are recognizable: high, in which males provide direct care by actively incubating and/or feeding young at rates equal to, or even greater than, the female; and low, in which males provide an escort or predator-defense function or provide no parental care at all. If male-male aggression is high and parental care is low, then T levels should be high throughout the breeding season. As male-male aggression decreases and parental care increases, the period of high circulating levels of T should become shorter and the amplitude of the increase less. In multiple-brooded populations, there may be several peaks of T as periods of male-male aggression alternate with parental phases (for the double-brooded case, see fig. 5ii, iv).

Of the more than 20 species of birds studied thus far under natural, or close to

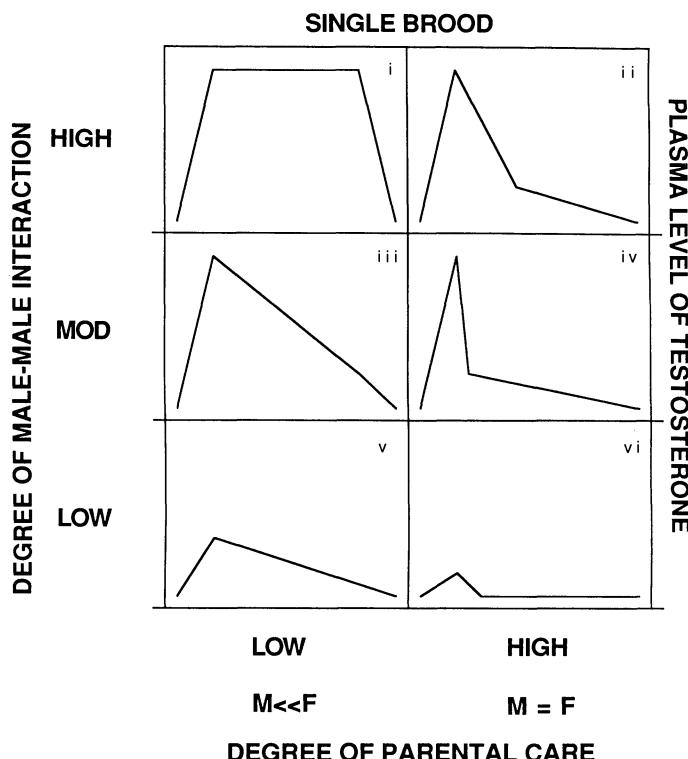


FIG. 4.—Theoretical patterns (*i–iv*) of circulating levels of testosterone (T) in male birds in relation to the degree of male-male interaction (high, moderate, low) and the degree of parental care provided by the male (feeding of young, brooding, etc.). Thus, high male-male interaction and low parental care (*i*) result in maximum levels of T throughout the season, whereas low male-male interaction and high parental care (*vi*) result in a low amplitude of T.

natural, breeding conditions, all fit one of the relationship models represented in figures 4 and 5. For example, male turkeys (*Meleagris gallopavo*; see Lisano and Kennamer 1977) and capercaillie (*Tetrao urogallus*; see Hissa et al. 1983) show extended male-male aggression (exploded-lek system) and provide no parental care. These males have temporal patterns of T that fit figure 4*i*. Conversely, male western gulls (*Larus occidentalis wymani*) incubate and feed young but do not have to compete for territories or mates (both are in excess; see Wingfield et al. 1982). The temporal pattern of T is of low amplitude and fits the theoretical relationship shown in figure 4*vi*.

Variation among and within Individuals

The patterns of T secretion outlined above are, of necessity, idealized and assume that each individual progresses through a breeding season without disruption. Conditions for breeding are rarely perfect, however, and an individual may lose a nest to a predator or storm (see Wingfield et al. 1983; Wingfield 1985b),

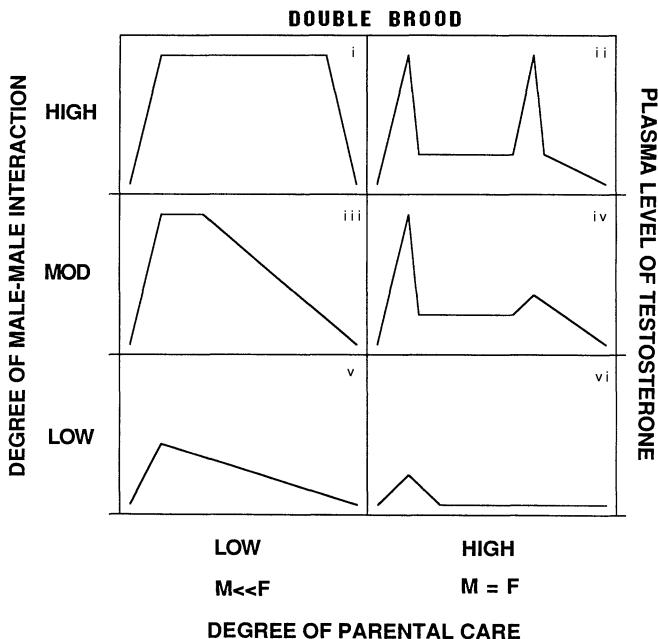


FIG. 5.—Theoretical patterns (*i–iv*) of circulating levels of testosterone (T) in double-brooded populations of male birds in relation to the degree of male-male interaction and the degree of parental care provided by the male. As in fig. 4, high male-male interaction and low parental care (*i*) predict maximum levels of T throughout the breeding season (although more extended than in fig. 4), whereas low male-male interaction and high parental care (*vi*) suggest a low-amplitude pattern. Subsequent surges of T with varying amplitude may occur with each clutch. Only two clutches are represented here; in species that raise three or more clutches, there may be three or more peaks in T (see, e.g., Hegner and Wingfield 1986).

may show increased levels of T as population density increases (Ball and Wingfield 1987), or may be challenged at unpredictable times within a breeding season (Wingfield 1985a). Thus, it is likely that temporal patterns of T vary to some degree among individuals within a population and, within an individual, from one breeding season to the next. The trade-off between male-male aggression and parental care again can be used to predict individual variation. This is shown in figure 6 for males of one species, the song sparrow (from Wingfield 1988). The top panel (fig. 6*i*) outlines the “normal” (or idealized) pattern of T in the absence of any perturbations (see, e.g., Wingfield 1984a). Variations in population density can affect male-male aggression, however, and thus the increase in T above *b* early in the season (fig. 6*ii*, from Wingfield and T. P. Hahn, unpublished manuscript; see also Ball and Wingfield 1987). Similarly, renesting after the loss of a clutch or brood results in a surge of T (during mate guarding for the replacement clutch; see Wingfield 1985b) above *b* at any time in the season (fig. 6*iii*). Challenges can have the same effect (fig. 6*iv*, from Wingfield 1985a); and in the most complex situation, challenges and renesting may result in multiple peaks of T above *b* (fig. 6*v*, inferred from investigations cited above). Thus, the theoretical

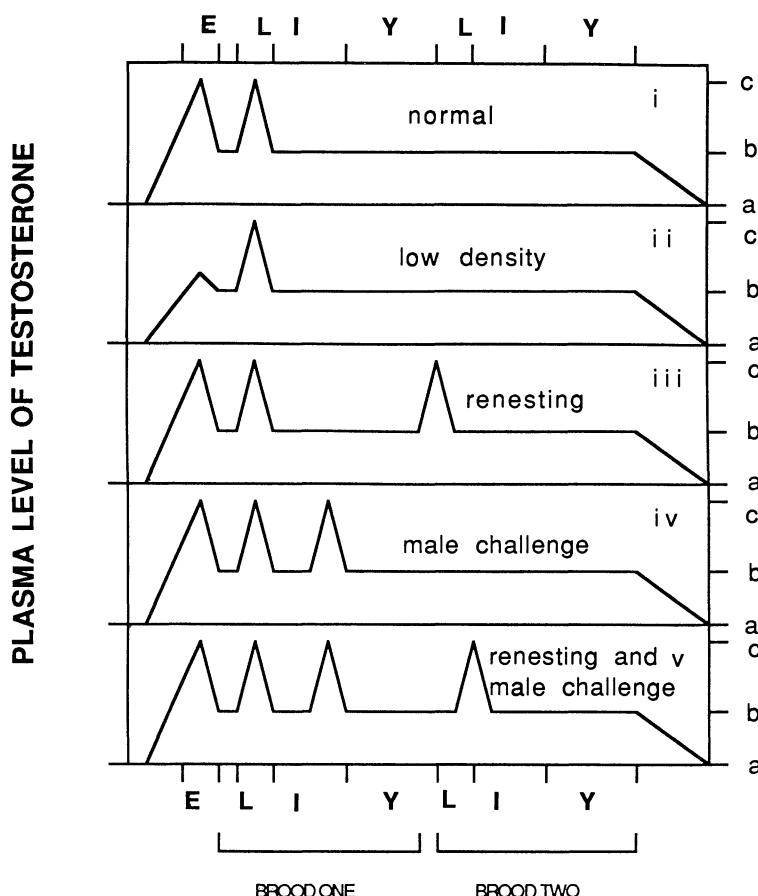


FIG. 6.—Circulating levels during a breeding season of testosterone levels in blood for male song sparrows, *Melospiza melodia*. The patterns represent both variation among individuals within a population under a variety of circumstances and variation within an individual from year to year (modified from Wingfield 1988). *E*, Establishing a territory; *L*, egg-laying period; *I*, incubation; *Y*, feeding young. Two broods are depicted. Testosterone levels as in fig. 1. *i*, A normal ("idealized") pattern (see, e.g., Wingfield 1984b); *ii*, low density leads to reduced male-male interaction (Wingfield and T. P. Hahn, unpublished manuscript; see also Ball and Wingfield 1987); *iii*, renesting occurs after loss of clutch or brood (Wingfield 1985b); *iv*, male challenges can occur (Wingfield 1985a); *v*, both renesting and male challenges make up the most complex scenario. Note that peaks of T during renesting and male challenges are unpredictable in time.

framework provided by the relationship between the degree of male-male aggression and the level of parental care predicts the temporal pattern of T secretion to be expected. This framework thus provides a valuable base both for elucidating the mechanisms that regulate reproductive development and behavior and for designing experiments to test the effects of the manipulation of T patterns in free-living birds.

*Environmental versus Genetic Determinants of Testosterone Level:
Responsiveness to Environmental Cues*

The transitory increases of T level above b result from stimulation by environmental cues, especially (and perhaps restricted to) male-male interactions and the effects of sexually receptive females. The duration and amplitude of this response depends also upon the degree of parental care displayed by a particular male. In males that provide no parental care (typically polygynous species or brood parasites), the tendency is for a greater responsiveness to interactions with other males and with receptive females than is the case for parental males. Thus, we expect prolonged high levels of T in nonparental males and low levels of T in parental males. This could explain some of the individual variations in the temporal patterns of T reported in the literature and summarized above. To test this idea, comparisons of c and b in relation to the degrees of male-male interaction and parental care displayed by individual males are necessary. The increment in T levels induced by photoperiod (or by endogenous cyclicity) to achieve a breeding baseline is represented by $b - a$ (see fig. 1). Thus, the extent to which T levels can potentially increase above b can be expressed by $(c - a)/(b - a)$, the ratio of the maximum level, c , and the breeding baseline, b , corrected for the nonbreeding baseline, a , which in most species is close to zero.

Next, rank-order indexes for the degree of male-male aggression and parental care (denoted by d) must be estimated from figures 4 and 5. We can give low, medium, and high scores for male-male interaction (1, 2, 3), thus representing increasing levels of aggression, and low and high scores for parental care (1, 2), thus representing increasing provisioning, such as feeding and brooding. An index can be derived for each species from the estimated ratio of degrees of male-male aggression and of parental care. For example, the turkey shows high aggression (3) and low parental care (1); thus, $d \approx 3$. The western gull shows low aggression (1) and high parental care (2); for this bird, $d \approx 0.5$. Although these rank-order indexes are arbitrary, they provide a consistent method for comparing male-male aggression and parental behavior across species.

Figure 7 shows the ratio of $c - a$ and $b - a$ versus d for 20 species for which we have sufficient data. Indexes for $c - a$ and $b - a$ were estimated by using known values for field maxima and peak levels in captivity (e.g., during photoperiod experiments) or by comparing peak levels of T during mate guarding or territory establishment with the maintenance levels of T during incubation or feeding of young.

A strong negative relationship emerges between responsiveness to behavioral cues ($[c - a]/[b - a]$; i.e., hormonal responsiveness) and the degrees of male-male interaction and parental behavior (d ; see fig. 7). Note that species tending toward polygyny (and one brood parasite) cluster at the lower end of the line, whereas species tending toward monogamy gather near the upper end of the curve. Males from two polyandrous species have values well within those for monogamy (it is perhaps reasonable to assume that since males of polyandrous species mate with one female, they are monogamous). Three species tend toward polygyny and overlap with monogamous species: *Sturnella neglecta*, *Pooecetes*

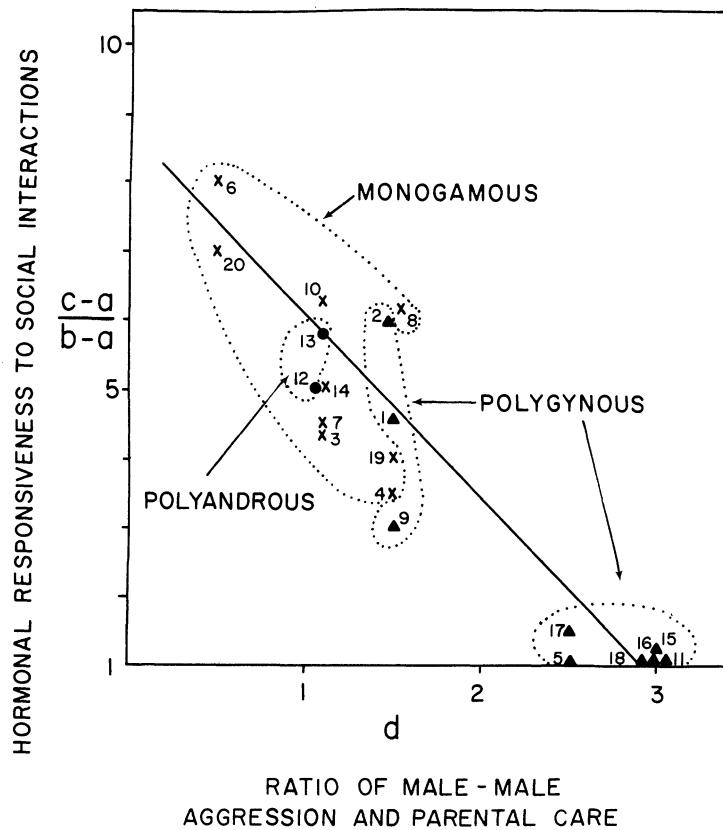


FIG. 7.—The relationship of responsiveness to behavioral interactions (increased testosterone levels above the breeding-season baseline, i.e., the ratio of $c - a$ to $b - a$) and the ratio of male-male interaction and degree of parental care (d). The negative correlation suggests that more-aggressive (less-parental) males are less responsive to behavioral interactions than are more-parental males. Polygynous species and the brood-parasitic cowbird (no. 5) tend to fall at the lower end of the line, but in two clusters, and monogamous species clump higher on the line. Polyandrous species fall wholly within the range of monogamous species. The numbers against each point represent individual species: 1, *Sturnella neglecta* (Wingfield and Farner 1980c); 2, *Pooecetes gramineus* (Wingfield and Farner 1980c); 3, *Sturnus vulgaris* (Ball and Wingfield 1987); 4, *Melospiza melodia* (Wingfield 1984b); 5, *Molothrus ater* (Dufly and Wingfield 1986a,b); 6, *Larus occidentalis wymani* (Wingfield et al. 1982); 7, *Zonotrichia leucophrys* (Wingfield and Farner 1978a,b); 8, *Passer domesticus* (Hegner and Wingfield 1986); 9, *Ficedula hypoleuca* (Silverin and Wingfield 1982); 10, *Turdus merula* (Schwabl et al. 1980); 11, *Meleagris gallopavo* (Lisano and Kennamer 1977); 12, *Actitis macularia* (Fivizzani and Oring 1986); 13, *Phalaropus tricolor* (Fivizzani et al. 1986); 14, *Diomedea exulans* (Hector et al. 1986); 15, *Phasianus colchicus* (Sakai and Ishii 1986); 16, *Coturnix coturnix* (Delville et al. 1984; Ramenofsky 1984); 17, *Agelaius phoeniceus* (Kerlan and Jaffe 1974; Beletsky et al. 1988); 18, *Lagopus lagopus* (Stokkan and Sharp 1980); 19, *Streptopelia risoria* (Feder et al. 1977); 20, *Aptenodytes forsteri* (Groscolas et al. 1988).

gramineus, and *Ficedula hypoleuca*, all of which have male parental care. The remaining polygynous species have no male parental care and cluster toward the bottom of the curve. The original prediction was that males withholding parental care (e.g., brood parasites and polygynous species, $d \approx 2 - 3$) would be more responsive to social stimuli (male-male aggression and sexual behavior of females) in terms of T secretion above level b ($[c - a]/[b - a]$). However, the theoretical relationships presented in figure 7 clearly suggest the opposite conclusion.

This counterintuitive finding may explain yet more controversy in the literature. Both male challenges in song sparrows and increased population density (and thus the frequency of male-male interactions) in starlings are accompanied by increases in T secretion above level b (Wingfield 1985a; Ball and Wingfield 1987). However, Harding and Follett (1979) were unable to show an increase in T after challenge with a decoy male in red-winged blackbirds (*Agelaius phoeniceus*). Similarly, an increase could not be shown in the T levels of adult males following exposure to females in red grouse (*Lagopus lagopus*), Japanese quail (*Coturnix coturnix japonica*), or brown-headed cowbird (Stokkan and Sharp 1980; Delville et al. 1984; Dufty and Wingfield 1986b). Since grouse, quail, and cowbirds are highly aggressive, show low or no parental care, and tend to polygyny, they fall toward the bottom of the line in figure 7, whereas the two responsive species (song sparrow and European starling, *Sturnus vulgaris*) lie higher on the curve. It is also of interest to note that territorial male lizards (*Sceloporus jarrovi*), which are polygynous and provide no parental care, also failed to increase plasma levels of T when challenged by conspecific males (Moore 1986). Thus, it is possible that this theoretical approach may have wide applications for vertebrates in general.

These data suggest that males of species that fall low on the curve are less responsive to behavioral cues (affecting the secretion of T) because there has been selection for T levels to be high throughout the breeding season (i.e., $c - a = b - a$). This situation appears to be typical with polygyny and brood parasites. It is possible that photoperiodic cues or endogenous rhythms of reproductive activity regulate T secretion to a maximum effective level and that social cues have no further effect. Higher on the curve, males are increasingly responsive to behavioral cues affecting the secretion of T (i.e., $c - a \gg b - a$). Since these males all show high parental care, levels of T tend to be lower (at level b) for much of the breeding season. However, mechanisms exist to increase the T level to c when necessary (such as a challenge from an intruding male), and responsiveness to social cues provides the correct context and specificity of that response.

Clearly, these data demonstrate that absolute levels of T do not always indicate reproductive state or correlate with aggression and mating system. Changes in T level (between b and c) are much more useful in making predictions about the endocrine basis of mating systems and breeding strategies. Much remains to be done to confirm this relationship, but the model can be tested by investigating responses to a challenging male or receptive female both in the field and in the laboratory. Thus, the extent to which an individual can elevate T between b and c , or whether $b = c$, can easily be determined. Correlates at the neural level, if any, are completely unknown but are potentially a rich source of research directions.

The theoretical approach we propose may help explain the diversity of temporal

patterns of T secretion in male birds, and perhaps all vertebrates, as a function of the degrees of male-male aggression and paternal behavior. This, in turn, correlates strongly with mating systems and breeding strategies. Furthermore, the models predict that mating systems will be found to vary as a function of endocrine responsiveness to behavioral cues that stimulate T levels above b . In polygynous males, it seems unlikely that high levels of male-male aggression or the presence of sexually receptive females throughout the breeding season elevates T levels further. The basis for this assumption is that the plasma levels of T in captive birds deprived of such stimuli are similar to those of free-living males (i.e., $b = c$). Rather, it appears that, in polygynous males, T levels are much less responsive to such cues, suggesting that the pattern of T is largely genetically determined and that there has been selection for males that have the maximum levels of T regardless of social situations. Monogamous males, in contrast, have temporal patterns determined to a great extent by behavioral cues rather than solely by endogenous factors.

Using the models as a framework, we can begin a new approach to elucidating the mechanisms underlying the extremely plastic responses of neural and neuro-endocrine systems to internal and external information (i.e., social interactions) during reproduction. In addition, manipulations of social states (by implants of hormones or other techniques) could be better designed using these models as guides and could provide powerful tools for determining ultimate causation in reproductive aspects of behavioral ecology as conceptualized by, for example, Orians (1969), Trivers (1972), and Emlen and Oring (1977).

SUMMARY

A combination of field and laboratory investigations has revealed that the temporal patterns of testosterone (T) levels in blood can vary markedly among populations and individuals, and even within individuals from one year to the next. Although T is known to regulate reproductive behavior (both sexual and aggressive) and thus could be expected to correlate with mating systems, it is clear that the absolute levels of T in blood are not always indicative of reproductive state. Rather, the pattern and amplitude of change in T levels are far more useful in making predictions about the hormonal basis of mating systems and breeding strategies. In these contexts we present a model that compares the amplitude of change in T level with the degree of parental care shown by individual males. On the basis of data collected from male birds breeding in natural or captive conditions, polygynous males appear less responsive to social environmental cues than are monogamous males. This model indicates that there may be widely different hormonal responses to male-male and male-female interactions and presumably equally plastic neural mechanisms for the transduction of these signals into endocrine secretions. Furthermore, evidence from other vertebrate taxa suggests strongly that the model is applicable to other classes.

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LITERATURE CITED

- Ball, G. F., and J. C. Wingfield. 1987. Changes in plasma levels of sex steroids in relation to multiple broodiness and nest site density in male starlings. *Physiol. Zool.* 60:191–199.
- Balthazart, J. 1983. Hormonal correlates of behavior. *Avian Biol.* 7:221–365.
- Beletsky, L. D., G. H. Orians, and J. C. Wingfield. 1988. Steroid hormones and polygyny: relationships to territorial status, breeding experience, and reproductive success in male red-winged blackbirds. *Auk* 106:107–117.
- Brown, N. L., and B. K. Follett. 1977. Effects of androgen on the testis of intact and hypophysectomized Japanese quail. *Gen. Comp. Endocrinol.* 33:267–277.
- Cardwell, J. R. 1989. Behavioral endocrinology of the spotlight parrotfish, *Sparisoma viride*, Scaridae, a protogynous coral reef fish. Ph.D. diss. University of British Columbia, Vancouver.
- Crews, D. 1984. Gamete production, sex hormone secretion, and mating behavior uncoupled. *Horm. Behav.* 18:22–28.
- Crews, D., and M. C. Moore. 1986. Evolution of mechanisms controlling mating behavior. *Science* (Washington, D.C.) 231:121–125.
- Delville, Y., J. Sulon, J.-C. Hendrick, and J. Balthazart. 1984. Effect of the presence of females on the pituitary-testicular activity in male Japanese quail (*Coturnix coturnix japonica*). *Gen. Comp. Endocrinol.* 55:295–305.
- Dittami, J. P., and H.-U. Reyer. 1984. A factor analysis of seasonal behavioral hormonal and body-weight changes in adult male bar-headed geese, *Anser indicus*. *Behaviour* 90:114–124.
- Donham, R. S., J. C. Wingfield, P. W. Mattocks, Jr., and D. S. Farner. 1982. Changes in testicular and plasma androgens with photoperiodically induced increase in plasma LH in the house sparrow. *Gen. Comp. Endocrinol.* 48:342–347.
- Dufry, A. M. 1989. Testosterone and survival: a cost of aggressiveness? *Horm. Behav.* 23:185–193.
- Dufry, A. M., Jr., and J. C. Wingfield. 1986a. Temporal patterns of circulating LH and steroid hormones in a brood parasite, the brown-headed cowbird, *Molothrus ater*. I. Males. *J. Zool. (Lond.) A* 208:191–203.
- . 1986b. The influence of social cues on the reproductive endocrinology of male brown-headed cowbirds: field and laboratory studies. *Horm. Behav.* 20:222–234.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* (Washington, D.C.) 197:215–223.
- Feder, H. H., A. Storey, D. Goodwin, C. Reboulleau, and R. Silver. 1977. Testosterone and 5-alpha-dihydrotestosterone levels in peripheral plasma of male and female ring doves (*Streptopelia risoria*) during the reproductive cycle. *Biol. Reprod.* 16:666–677.
- Fivizzani, A. J., and L. W. Oring. 1986. Plasma steroid hormone levels in free-living spotted sandpipers, *Actitis macularia*. *Biol. Reprod.* 35:1195–1201.
- Fivizzani, A. J., M. A. Colwell, and L. W. Oring. 1986. Plasma steroid hormone levels in free-living Wilson's phalaropes, *Phalaropus tricolor*. *Gen. Comp. Endocrinol.* 62:137–144.
- Groscolas, R., M. Jallageas, J. Leloup, and A. R. Goldsmith. 1988. The endocrine control of reproduction in male and female emperor penguins (*Aptenodytes forsteri*). Pages 1692–1701 in H. Ouellet, ed. *Acta XIX Congressus Internationalis Ornithologici*. Vol. 2. University of Ottawa Press, Ottawa.
- Harding, C. H., and B. K. Follett. 1979. Hormone changes triggered by aggression in a natural population of blackbirds. *Science* (Washington, D.C.) 203:918–920.
- Harding, C. H. 1981. Social modulation of circulating hormone levels in the male. *Am. Zool.* 21: 223–232.
- Harvey, S., J. G. Phillips, A. Rees, and T. R. Hall. 1984. Stress and adrenal function. *J. Exp. Zool.* 232:633–646.
- Hector, J. A. L., J. P. Croxall, and B. K. Follett. 1986. Reproductive endocrinology of the wandering

- albatross, *Diomedea exulans*, in relation to biennial breeding and deferred sexual maturity. *Ibis* 128:9–22.
- Hegner, R. E., and J. C. Wingfield. 1986. Behavioral and endocrine correlates of multiple brooding in the semi-colonial house sparrow, *Passer domesticus*. I. Males. *Horm. Behav.* 20:294–312.
- . 1987. Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk* 104:462–469.
- Hissa, R., S. Saarela, J. Balthazart, and R. J. Etches. 1983. Annual variation in the concentrations of circulating hormones in capercaillie (*Tetrao urogallus*). *Gen. Comp. Endocrinol.* 51:183–190.
- Kerlan, J. T., and R. B. Jaffe. 1974. Plasma testosterone levels during the testicular cycle of the red-winged blackbird (*Agelaius phoeniceus*). *Gen. Comp. Endocrinol.* 22:428–432.
- Lisano, M. E., and J. E. Kennamer. 1977. Seasonal variations in plasma testosterone level in male eastern wild turkeys. *J. Wildl. Manage.* 41:184–188.
- Marler, C. A., and M. C. Moore. 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behav. Ecol. Sociobiol.* 23:21–26.
- Moore, M. C. 1982. Hormonal responses of free-living male white-crowned sparrows to experimental manipulation of female sexual behavior. *Horm. Behav.* 16:323–329.
- . 1983. Effect of female sexual displays on the endocrine physiology and behavior of male white-crowned sparrows, *Zonotrichia leucophrys*. *J. Zool. (Lond.)* 199:137–148.
- . 1986. Circulating steroid hormones during rapid aggressive responses of territorial male mountain spiny lizards, *Sceloporus jarrovi*. *Horm. Behav.* 21:511–521.
- . 1988. Testosterone control of territorial behavior: tonic-release implants fully restore seasonal and short-term aggressive responses in free-living castrated lizards. *Gen. Comp. Endocrinol.* 70:450–459.
- Moore, M. C., and R. Kranz. 1983. Evidence for androgen independence of male mounting behavior in white-crowned sparrows (*Zonotrichia leucophrys gambelii*). *Horm. Behav.* 17:414–423.
- Moyer, K. E. 1968. Kinds of aggression and their physiological basis. *Commun. Behav. Biol. Part A, Orig. Artic.* 2:65–87.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589–603.
- Ramenofsky, M. 1984. Agonistic behavior and endogenous plasma hormones in male Japanese quail. *Anim. Behav.* 32:698–708.
- Sakai, H., and S. Ishii. 1986. Annual cycles of plasma gonadotropins and sex steroids in Japanese common pheasants, *Phasianus colchicus versicolor*. *Gen. Comp. Endocrinol.* 63:275–283.
- Schwabl, H., J. C. Wingfield, and D. S. Farner. 1980. Seasonal variations in plasma levels of luteinizing hormone and steroid hormones in the European blackbird, *Turdus merula*. *Vogelwarte* 30:283–294.
- Siegel, H. S. 1980. Physiological stress in birds. *BioScience* 30:529–534.
- Silver, R., H. Andrews, and G. F. Ball. 1985. Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *Am. Zool.* 25:823–840.
- Silverin, B. 1980. Effects of long-acting testosterone treatment on free-living pied flycatchers, *Ficedula hypoleuca*, during the breeding period. *Anim. Behav.* 28:906–912.
- Silverin, B., and J. C. Wingfield. 1982. Patterns of breeding behavior and plasma levels of hormones in a free-living population of pied flycatchers, *Ficedula hypoleuca*. *J. Zool. (Lond.)* 198: 117–129.
- Stokkan, K.-A. and P. J. Sharp. 1980. Seasonal changes in the concentrations of plasma luteinizing hormone and testosterone in willow ptarmigan (*Lagopus lagopus lagopus*) with observations on the effects of short days. *Gen. Comp. Endocrinol.* 40:109–115.
- Townsend, D. S., and W. H. Moger. 1987. Plasma androgen levels during male parental care in a tropical frog (*Eleutherodactylus*). *Horm. Behav.* 21:93–99.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Aldine, Chicago.
- Wingfield, J. C. 1980. Fine temporal adjustment of reproductive functions. Pages 367–389 in A. Epple and M. H. Stetson, eds. *Avian endocrinology*. Academic Press, New York.
- . 1983. Environmental and endocrine control of reproduction: an ecological approach. Pages 265–288 in S.-I. Mikami, S. Ishii, and M. Wada, eds. *Avian endocrinology: environmental and ecological aspects*. Japanese Scientific Societies Press, Tokyo; Springer, Berlin.

- _____. 1984a. Androgens and mating systems: testosterone-induced polygyny in normally monogamous birds. *Auk* 101:665–671.
- _____. 1984b. Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. I. Temporal organization of the reproductive cycle. *Gen. Comp. Endocrinol.* 56:406–416.
- _____. 1985a. Short term changes in plasma levels of hormones during establishment and defense of a breeding territory in male song sparrows, *Melospiza melodia*. *Horm. Behav.* 19:174–187.
- _____. 1985b. Influences of weather on reproduction in male song sparrows, *Melospiza melodia*. *J. Zool. (Lond.) A* 205:525–544.
- _____. 1988. The challenge hypothesis: interrelationships of testosterone and behavior. Pages 1685–1691 in H. Ouellet, ed. *Acta XIX Congressus Internationalis Ornithologici*. Vol. 2. University of Ottawa Press, Ottawa.
- Wingfield, J. C., and D. S. Farner. 1976. Avian endocrinology—field investigations and methods. *Condor* 78:570–573.
- _____. 1978a. The endocrinology of a naturally breeding population of white-crowned sparrow, *Zonotrichia leucophrys pugetensis*. *Physiol. Zool.* 51:188–205.
- _____. 1978b. Annual cycles of luteinizing hormone and sex steroid hormones in the plasma of the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *Biol. Reprod.* 19:1046–1056.
- _____. 1979. Endocrine correlates of renesting after loss of clutch or brood in the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *Gen. Comp. Endocrinol.* 38:322–331.
- _____. 1980a. Control of seasonal reproduction on temperate zone birds. *Prog. Reprod. Biol.* 5:62–101.
- _____. 1980b. Temporal aspects of the secretion of luteinizing hormone and androgen in the white-crowned sparrow, *Zonotrichia leucophrys*. Pages 463–467 in R. Nöhring, ed. *Acta XVIII Congressus Internationalis Ornithologici*. Deutschen Ornithologen, Berlin.
- _____. 1980c. Endocrinologic and reproductive states of bird populations under environmental stress. E.P.A. Rep., contract no. cc699095.
- Wingfield, J. C., and P. Marler. 1988. Endocrine basis of communication: reproduction and aggression. Pages 1647–1677 in E. Knobil and J. D. Neill, eds. *The physiology of reproduction*. Raven, New York.
- Wingfield, J. C., and M. C. Moore. 1987. Hormonal, social, and environmental factors in the reproductive biology of free-living male birds. Pages 149–175 in D. Crews, ed. *Psychobiology of reproductive behavior: an evolutionary perspective*. Prentice-Hall, Englewood Cliffs, N.J.
- Wingfield, J. C., and M. Ramenofsky. 1985. Hormonal and environmental control of aggression in birds. Pages 92–104 in R. Gilles and J. Balthazart, eds. *Neurobiology*. Springer, Berlin.
- Wingfield, J. C., A. Newman, G. L. Hunt, and D. S. Farner. 1982. Endocrine correlates of female-female pairing in the western gull, *Larus occidentalis wymani*. *Anim. Behav.* 30:9–22.
- Wingfield, J. C., M. C. Moore, and D. S. Farner. 1983. Endocrine responses to inclement weather in naturally breeding populations of white-crowned sparrows. *Auk* 100:56–62.
- Wingfield, J. C., G. F. Ball, A. M. Dufty, R. E. Hegner, and M. Ramenofsky. 1987. Testosterone and aggression in birds: tests of the challenge hypothesis. *Am. Sci.* 75:602–608.
- Witschi, E. 1961. Sex and secondary sexual characters. Pages 115–168 in A. J. Marshall, ed. *Biology and comparative physiology of birds*. Academic Press, New York.