ing T level following cessation of prolonged marital stress? As M&B state, the break-up of a marriage usually spans years, "accompanied by arguments and confrontations" (sect. 9). Hormone levels are multiply determined, and choosing a single crude demographic measure such as marital status ("because there was little behavioral measurement in the study") and looking for endocrine associations is unlikely to lead to significant advances in our knowledge of endocrine–behaviour relationships in man.

In conclusion, the link between T and aggressive and sexual behaviour in lower animals (e.g., rodents) is clearly established. However, as we ascend the phylogenetic ladder to humans, this relationship becomes less clear. This is not to deny that such a relationship exists, but the complexity of human social behaviour suggests that both behaviour and endocrine status are influenced by a wide variety of biological and psychological variables, and a multivariate approach is required. Furthermore, as a consequence of the pulsatile variability in circulating T levels in man, significant error variance is introduced into single-sample correlational studies. Definitive evidence is likely to come from placebo-controlled, double-blind experiments in which circulating T levels are manipulated and appropriately reliable and sensitive assays of behaviour are taken.

Of fish and men: A comparative approach to androgens and social dominance

Rui F. Oliveira

Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, 1100 Lisboa, Portugal. **ruiol@ispa.pt**

Abstract: Four aspects of Mazur & Booth's target article are discussed from a comparative perspective using teleost fish as a reference: (a) the relationship between aggression, dominance, and androgens; (b) the interpretation of the data in light of the challenge hypothesis; (c) the potential role of testosterone as a physiological mediator between social status and the expression of male characters; and (d) the fact that metabolic conversions of testosterone may be important in its effect on aggression/dominance.

As a fish biologist interested in hormones and behavior, I was fascinated to find myself to some extent on very familiar ground while reading Mazur & Booth's (M&B's) target article on dominance and testosterone in humans. However, insofar as testosterone (T) in particular and androgens in general are an essential part of the conserved vertebrate reproductive axis (i.e., hypothalamus–pituitary–gonads), one would expect some parallels between teleosts and mammals, including humans, in the relationships between sex hormones and social behavior (although M&B neglect to acknowledge the comparative literature on androgens and dominance in nonprimate vertebrates). Here I will comment on four issues raised by M&B in the light of this comparative approach, using the teleosts as counterpoint. Teleost fishes are the most diverse of living vertebrate taxa and represent a very successful lineage of recently evolving organisms (Nelson 1994). It would accordingly be very interesting to compare hormone–behavior systems in these two successful vertebrate lineages.

Dominance, aggression, and androgens. In the target article, M&B point out that dominance in humans may be exerted nonaggressively and that T is related primarily to dominance and not to aggression per se, except when dominance is asserted aggressively. They go on to suggest that nearly all primate studies linking T to aggressive behavior can also be seen as linking T to social dominance.

In fish, castration lowers both androgen and aggression levels but not social dominance (Francis et al. 1992). These results can be explained by the fact that aggression is an individual attribute, whereas social dominance is a relational one, which can vary with the social context into which the individual is placed (Bernstein 1981; Francis 1988). [See also Bernstein: "Dominance Relationships and Ranks" *BBS* 3 1981.] Moreover, the underlying mechanisms involved in dominance relationships may differ according to the number of individuals involved. In dyads, dominance may be more directly related to aggression, because the two individuals are competing directly, whereas, in triads, other phenomena may be involved, such as prior experience, individual recognition, bystander effects, or transitive inference. It would accordingly be expected that, in cases in which dominance is assessed in a dyad, T can be more easily related to aggression. Nevertheless, T is also known to be related to attention/cognitive mechanisms (Hampson & Kimura 1992), which might also be involved in status-assessment processes; thus T could still be linked to dominance in this scenario. The findings linking T to aggression but not to social dominance in fish can thus be explained as a resilience effect of the dominance relationship previously established between each pair of tested individuals. It would therefore be instructive to pay more attention to the context in which the data are collected and to the possible underlying mechanisms involved in status acquisition, in considering the relationship between T and dominance.

The challenge hypothesis. Wingfield (1984) has proposed that the androgen levels of a given individual will respond in the short term to the social interactions in which the animal has participated, which will result in an adjustment of the readiness and intensity of the agonistic behavior according to changes in the social environment into which the animal is placed. In this view, variation in T levels may be more closely associated with temporal variations in aggression than with basal reproductive physiology. According to the challenge hypothesis, baseline breeding levels of T are sufficient for normal reproductive function and temporal patterns in T levels may differ between species according to the mating system of the population. In monogamous species, T levels should rise above the baseline breeding level only in periods of social challenge, so that aggression will not interfere with parental care and pair bonding, whereas, in polygynous species, T levels should increase to near the maximal level and remain high, because this will facilitate aggressive behaviors in male–male competition (Wingfield et al. 1990). As the human species is considered to be monogamous and does not present a breeding seasonality, the challenge hypothesis would predict human male T levels to respond sharply to social challenges. In fact, the data presented by M&B provide further evidence for the challenge hypothesis; T rises in response to a competitive match, as if in anticipation of the challenge. This precontest rise in T might have the function of preparing the individuals for confrontation by increasing readiness to fight and improving the cognitive capabilities required by a competitive situation.

Again, there are parallel data for teleosts. Socially isolated males show low levels of both aggression and plasma androgens; these levels increase very rapidly after visual exposure to a territorial male, which acts as a challenge stimulus (Hannes & Franck 1983; Heiligenberg & Kramer 1972). Territorial males have higher androgen levels than nonterritorial males, and recently established territorial males undergo a large increase in androgen levels. After territory establishment, androgen levels drop to the territorial male baseline. Furthermore, simulated territorial intrusions promote an increase in androgen levels in resident males (Barnett & Pankhurst 1994; Cardwell & Liley 1991; Oliveira et al. 1996). This link between androgens and social status has also been shown to be a function of the number of territorial intrusions and of population density (Pankhurst & Barnett 1993). These data suggest that short-term increases in circulating androgens are a response to intense social competition during territory establishment. It must be of high adaptive value to react to the presence of a male intruder with a quick rise in agonistic motivation, which might be achieved by high androgen levels. Subordinate individuals should adjust their aggressive behavior to a level that maximizes their reproductive success without promoting excessive confrontations with dominant males. This trade-off may be regulated by social modulation of androgen levels.

Androgens, social dominance, and sexual selection. Androgens may play a very important proximate causal role as mediators between social status and the expression of male secondary sex characters, both morphological and behavioral (including aggressive behavior), which might serve as cues to both males and females. Indeed, increasing evidence shows that androgen levels are strongly affected by social factors such as the outcomes of social interactions in which the individual participates (see Oliveira et al. 1996, for references). On the other hand, the expression of many male secondary sex traits is under androgen control (for teleosts, see Borg 1994). Together, these results suggest a model in which androgens would rise in response to social status and would in turn activate both the expression of male reproductive behavior, including aggression, and the expression of male secondary sex characters. Dominant males, by signalling their status both morphologically and behaviorally, may reinforce their social status by a positive-feedback mechanism. This causal chain has been demonstrated for a cichlid fish by our group (Oliveira & Almada 1995; 1997; Oliveira et al. 1996). Thus, the expression of phenotypes, such as armaments and ornaments that are thought to evolve as a result of sexual selection, may be influenced by the social environment to which the individual is exposed, a fact that is usually ignored in genetic models of sexual selection.

Again, there are some human data to support this model. M&B provide some data in their target article (sect. 1) concerning the advantages of human dominance, which include mate attraction and earlier sexual activity (which could increase fitness). Moreover, M&B also suggest that "around puberty, the effect of T on behavior works primarily through long-term reorganization of the body, including increased size, muscle mass, and the appearance of secondary sexual characteristics" (sect. 3). It would thus be very interesting to know whether more dominant men reach puberty earlier and whether androgens are also implicated as mediators between social status and the expression of male secondary sex characters in humans, which might serve as cues available to other individuals too.

Testosterone: A hormone or a prohormone? M&B give an oversimplified picture of vertebrate androgens and their relationship to behavior. T has received considerable attention as a proximate factor regulating aggression and social dominance in vertebrates; however, an increasing body of evidence shows that, in the so-called higher vertebrates (i.e., birds and mammals), T has to be converted to an estrogen (E) metabolite for it to be effective in influencing behavior (Balthazart & Foidart 1993; Hutchison 1993; Schlinger & Callard 1990). For example, it has been shown in rats that administering an aromatase (the enzyme complex responsible for the metabolization of T into E) inhibitor together with T inhibits the demonstrated effect of T in promoting aggression (Brain et al. 1988).

In fish, the most potent androgen is a T metabolite, 11-ketotestosterone (11-KT), which is unique to fish and to urodeles (Kime 1987). Interestingly, in a study of steroid metabolism, it was demonstrated that keeping fish in high densities inhibits territorial and aggressive behaviors and also blocks the conversion of T to 11-KT. In the same study, Leitz (1987) showed that dominant males had a higher production of 11-oxy-androgens than subordinates. In another study, it was found that, when male groups were created, 11-KT increased in fish that became territorial but showed no change in nonterritorial fish, suggesting that one physiological consequence of subordinate status would be to block the enzyme that converts T into 11-KT (11β-hydroxylase), leading to a reduction in 11-KT production and an accumulation of T (Oliveira et al. 1996).

It is interesting that in humans there is also some evidence that metabolic conversions of hormones are important in their effects on aggression and/or dominance. In a study on androgens and different components of aggression in men, Christiansen and Knussmann (1987) found that interest in sexual aggression was not correlated with salivary or circulating levels of T but was negatively correlated with an index of conversion of T into one of its metabolites, dihydrotestosterone (DHT). Because the available evidence linking T to aggression and dominance in humans is mainly correlational, future research should also consider the role of T metabolism in the activation of aggressive and dominant behaviors.

I hope to have drawn attention to the fact that fish and men share a number of mechanisms underlying the hormone–behavior system of dominance and aggression, suggesting a conserved ancestral mechanism across all the vertebrate taxa. A comparative approach can contribute to a better understanding of the reciprocal relationship between hormones and behavior.

ACKNOWLEDGMENTS
The preparation of this commentary benefitted from support by JNICT (UI&D/331). The author thanks Teresa Avelar, who reviewed the manuscript.

The nurture of nature: Social, developmental, and environmental controls of aggression

Charles T. Snowdon
Department of Psychology, University of Wisconsin, Madison, WI 53706-1696. **snowdon@macc.wisc.edu**

Abstract: Evidence from many species suggests that social, developmental, and cognitive variables are important influences on aggression. Few direct activational or organizational effects of hormones on aggression and dominance are found in nonhuman primates. Female aggression and dominance are relatively frequent and occur with low testosterone levels. Social, cultural, and developmental mechanisms have more important influences on dominance and aggression than hormones.

Does testosterone (T) have a direct role in dominance and aggressive behavior in men? Much of the evidence presented is correlational and many of the correlations, though statistically significant, have small effect sizes, explaining a minuscule amount of variance. Two important sets of contrary data have been ignored: (1) Several studies of human and nonhuman animals indicate that social, environmental, and cognitive variables influence aggression to a greater degree than hormonal levels. (2) Females of many species, including humans, display a capacity for aggression at least equal to that of males despite much lower levels of T; there is also evidence that female reproductive success benefits directly from dominance.

Testing conditions often influence the outcome of dominance contests: Castrated male woodrats fight as vigorously as intact males in neutral arenas (Caldwell et al. 1984). In mice, castrated males with no previous fighting experience do poorly, but castrated males with fighting experience prior to castration show normal levels of aggression (Scott & Fredericson 1951). Bernstein et al. (1983) demonstrated that T levels in rhesus macaques changed in response to winning or losing a dominance contest, in parallel with results on humans reviewed by Mazur & Booth (M&B), but they found no change in T levels when monkeys were provoked to attacks against a human holding two infant monkeys over a much longer time period than the dominance contrast. Bernstein et al. (1983) suggest that a cognitive interpretation of an encounter may have more influence on hormones than the actual amount of aggression expressed. [See also Bernstein "Dominance" *BBS* 3 1981.]

Wallen (1996) reviewed 30 years of research on hormonal and social influences on behavior in rhesus macaques and concluded that social environments had a more important influence on the expression of dominance and submissive behaviors than did hormonal environment. The presence or absence of mothers and the sex composition of peer groups influenced all sexually dimorphic behaviors. Rough-and-tumble play was the only behavior found in high levels in males across all rearing conditions, but even this was