



## Commentary

**Advancing the Challenge Hypothesis**

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The Challenge Hypothesis has been a cornerstone of behavioral endocrinology since it was first proposed (Wingfield et al., 1990). This hypothesis originally sought to explain the complex seasonal patterns of androgens in birds. While there is a basic pattern of males having higher androgen levels during the breeding season than non-breeding season, males of many species also exhibit different baseline androgen levels during different breeding sub-stages and spikes in androgen levels associated with either social instability or female receptiveness. By investigating the social mating system, the degree of male–male aggression, and the degree of paternal care, Wingfield and colleagues developed predictions about how androgen levels should vary seasonally. Additionally, this work predicted how male birds should hormonally respond to social challenges from other males. Increases in plasma androgen levels in response to challenges would support further aggression. As of January 2007, the original Challenge Hypothesis paper has been cited over 400 times and predictions from the Challenge Hypothesis have been tested in all vertebrate classes. Indeed the Challenge Hypothesis has even been tested in humans (Archer, 2006)!

As the Challenge Hypothesis has been tested in species with varied life histories, the hypothesis has continued to evolve. Significant advances have occurred when investigators have attempted to look for trends and relationships across species in their androgen responsiveness (AR, the ratio of the breeding season maximum and breeding season baseline androgen concentrations). Two recent studies by Hirschenhauser and colleagues have analyzed androgen responsiveness across species and produced interesting results. Among avian species, when corrected for phylogenies, it appears that mating system is more important than degree of paternal care in predicting androgen responsiveness (Hirschenhauser et al., 2003). More recently, a quantitative meta-analysis of all vertebrate species tested under the Challenge Hypothesis found general support for

the hypothesis with some variation based on taxa (Hirschenhauser and Oliveira, 2006). These two studies were significant advances in our understanding of how androgen patterns vary with life history. As more species are tested, across broader taxonomic groups, these analyses will need to be repeated.

The study by Goymann, Landys and Wingfield (current issue) is another significant advance in the Challenge Hypothesis. Prior to this study, investigators have not always attempted to discriminate the causes of the increase in androgens above breeding baseline levels (defined as level B in the paper). The assumption was generally made that these high levels (defined as level C in the paper) were the result of social interactions, either male–male or male–female. The novelty of the current study is the attempt to discern the different triggers of elevated androgen levels. The authors suggest that there are two categories of triggers (environmental and social) and that androgen responses to these two types are fundamentally different and should be treated as independent variables. This new level of investigation in androgen responsiveness will hopefully elucidate some previous studies as well as give future studies a new avenue of investigation.

One interesting, and presumably unexpected, outcome of the Goymann et al. study is the apparent difference between single-brooded and multiple-brooded species in how they hormonally respond to social challenges. Single-brooded species appear to show a larger seasonal response of androgen levels but smaller (or no) response to male–male challenges, in comparison with multiple-brooded species. From these data, it appears that males of single-brooded species are ramping up androgen levels in anticipation of social challenges. This may occur because social challenges are fairly synchronous in timing in single-brooded species because they have limited time available to breed. Multiple-brooded species probably have a more extended breeding season and thus do not have a well-defined period of social challenges. As such, multiple-brooded species are hormonally responsive to male challenges whenever they

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occur. However, the relationship between brood number and responsiveness to male challenges is not universal. For example, the multiple-brooded rufous-collared sparrow (*Zonotrichia capensis*) does not show an androgen response to male challenges during the early or mid-breeding periods (Moore et al., 2004).

A nice aspect of the Goymann et al. paper is that, in addition to reviewing and synthesizing past studies, it presents a way forward. The authors propose a comprehensive series of observational and experimental studies that investigators can use to understand the behavioral role of androgens in their species. Much of this way forward is based on investigating androgen responsiveness ( $R$  in this paper) to a variety of stimuli. By documenting both breeding baseline and maximal levels of androgens in a population of males, an investigator can establish the range of possible androgens levels and thus the potential androgen responsiveness of males ( $R_{\text{potential}}$ ). Then, through experimental intrusions, the investigator can establish how responsive androgen levels in males are to other males ( $R_{\text{male-male}}$ ), females ( $R_{\text{male-female}}$ ) as well as other aspects of their environment ( $R_{\text{environment}}$ ). All of these steps are necessary to establish a complete understanding of the role of androgens in social behavior. However, because of the difficulty of collecting these data, all these steps have only been conducted in a few species so far. Hopefully more investigators will use this plan to conduct more complete studies of the role of androgens in social behavior.

So where do these recent studies leave us in terms of the Challenge Hypothesis? As stated before, the hypothesis is a foundation of behavioral endocrinology and yet is constantly evolving. As more species are investigated, our understanding of the role of androgens in mediating aggression will grow. For example, the role of androgens in the evolution of vertebrate life histories is an area of research receiving much more attention (Hau, 2007; Ricklefs and Wikelski, 2002). Three prominent avenues for further studies include investigating (1) a wider variety of taxa, (2) species that live in a wider variety of environments and (3) females. While the Challenge Hypothesis has been tested in all vertebrate classes, the vast majority of tests have occurred in birds. Other groups, especially fish with their wide variety of mating systems (Hirschenhauser et al., 2004; Oliveira et al., 2005), would surely present opportunities to refine the Challenge Hypothesis. In addition, the majority of studies of the Challenge Hypothesis have been conducted on temperate and arctic breeding animals that may have relatively brief breeding seasons and other environmental constraints on breeding (Wingfield, 2003; Wingfield and Hunt, 2002). The majority of vertebrates inhabit tropical latitudes and experience very different environmental conditions than temperate zone vertebrates. Thus, they may be expected to exhibit different hormone–behavior relationships (Goymann et al., 2004; Hau, 2001; Moore et al., 2004). Finally, females have been woefully understudied in terms of hormonal relationships with aggression (Elekovich and Wingfield, 2000; Goymann et al., 2001; Goymann and Wingfield, 2004; Ketterson et al., 2005; Woodley

and Moore, 1999a,b). Future investigations of females will surely expand our knowledge of hormone–behavior relationships, especially in terms of parental care and mating systems. Many of us look forward to seeing where the Challenge Hypothesis takes us next!

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