Hormones and Behavior 92 (2017) 9–12

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Review article

# The challenge hypothesis: Where it began and relevance to humans

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ARTICLE INFO

*Article history:*
Received 3 August 2016
Revised 6 November 2016
Accepted 9 November 2016
Available online 14 November 2016

ABSTRACT

A contribution to a special issue on Hormones and Human Competition.

Over 40 years ago assay methods that allowed the accurate measurement of circulating levels of hormones were developed for the first time enabling us to sample free-living as well as captive animals. This led to a new concept called "field endocrinology". It quickly became apparent that endocrine profiles of animals under natural conditions were very different from congeners in captivity. Furthermore, hormone data could be organized by functional units (e.g. reproductive states) spaced in time according to natural duration of those states rather than simply by date alone. This approach changed how we interpret data and revealed species-specific patterns of hormone secretion. The "challenge hypothesis", stating that the temporal patterns of testosterone in blood were determined by a trade-off between the degree of male-male competition that increased testosterone, and the expression of paternal care that required a decrease in testosterone, grew out of a combination of field endocrine investigations that then informed laboratory experimentation. A strong argument can now be made that the challenge hypothesis is highly relevant for understanding social interactions in humans and non-human primates. Investigations on human subjects provide some of the best models for the challenge hypothesis. However, the central mechanisms by which aggressive and other social interactions regulate the hypothalamo-pituitary-gonad axis will depend upon work on not only primates, but also other vertebrates in very different ecological contexts. Research on the challenge hypothesis in humans will play a critical role as new insight on the interrelationships of testosterone and male-male competition comes from new technologies.

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Throughout my career, I have been intrigued by how animals respond to changing environments, including social interactions. Growing up in rural Derbyshire, UK, I remember the winter of 1959/60 that was one of the coldest on record. I was eleven years old and interested in nature in general. That winter had profound effects on wildlife because snow cover and temperatures well below freezing persisted for months. Particularly fascinating were the arrivals of northern birds I had never seen before. The usual winter residents were leaving and others that were normally territorial began flocking and roosting communally, presumably to combat the severe cold. Observing these dramatic changes in social interactions set the stage for my later career interests in why and how animals regulate complex transitions in behavior. Because most birds are easy to observe and so much is known about their migrations and biology in general, these animals became the preferable study group for me. Although I conducted my Ph.D. work on marine fish, my focus on avian systems has persisted to this day.

Later on as an undergraduate and then during my graduate research I received training in comparative endocrinology. It quickly became clear to me that the regulation of behavior by hormones provided a suite of potential mechanisms underlying changing social behavior in response to environmental events in birds. Furthermore, avian endocrine systems are about 90% homologous with those of humans. Other animal models have since proven useful too, and I personally was delighted to see mammals, particularly primates, become models for endocrine investigations of social interactions in natural conditions.

In the 1970s it also became clear to me that to understand the mechanisms by which social interactions influence, and are influenced by,

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http://dx.doi.org/10.1016/j.yhbeh.2016.11.008
0018-506X/© 2016 Published by Elsevier Inc.

hormones depended upon significant breakthroughs in assay technology. The 1970s and 1980s saw the development of assay methods that allowed the accurate measurement of circulating levels of hormones, particularly steroids, for the first time (Wingfield and Farner, 1975). The assays were sufficiently sensitive to allow quantification of hormone titers in plasma samples small enough to be collected from a wide spectrum of vertebrates, including rodents and songbirds. In turn, these techniques made the collection of samples from free-living animals without debilitating them, so that further observations of individuals could be made in the field, and additionally enabled controlled field experiments to sample animals, often repeatedly, in environmental and social contexts (Harding and Follett, 1979). This new concept was called "field endocrinology" (Wingfield and Farner, 1976) and became established across all vertebrate taxa. As new data from free-living animals accumulated, it became obvious to me that endocrine profiles of animals under natural conditions were very different from congeners in captivity where the lack of environmental and social input in laboratory conditions was a major confound. Moreover, songbirds such as the song sparrow, *Melospiza melodia*, are ideal models as they are abundant, easy to catch and work with in the field and laboratory and, particularly important, there is a substantial literature on the behavior and endocrinology of this and similar species (e.g. Wingfield and Farner, 1993).

In the early days of my postdoctoral career another advantage of field endocrinology that occurred to me involved the collection of data that could then be organized by functional units (e.g. reproductive states) spaced in time according to the natural duration of those states rather than simply by date alone. I was greatly impressed with how this approach radically changed the interpretation of data and revealed species-specific patterns of hormone secretion, hitherto unknown, and markedly different from the patterns revealed simply by plotting over calendar time (Wingfield and Farner, 1993). An example is the correlation of circulating testosterone levels and aggression, especially among males in various reproductive states, with and without females being present. This new way of organizing testosterone levels in specific states (such as arrival, establishment of a territory, mating, incubation and feeding of young) revealed complex patterns with testosterone levels generally being high early in the season when most aggressive interactions occurred and much lower during the parental phase (Wingfield and Farner, 1993). Furthermore, we were then able to generate novel hypotheses such as "testosterone is incompatible with parental care in males" and conduct investigations on neuroendocrine and endocrine functions in relation to ecological factors, mating systems, and breeding strategies.

These data were a revelation to us and suggested new ways as to how environmental changes, physical and social, could drive patterns of hormone secretion that then adjust morphology, physiology and behavior to individual context and experience in the natural world. So many vertebrate species have now been studied in natural or semi-natural conditions that meta-analyses are possible (Hirschenhauser et al., 2003; Hirschenhauser and Oliviera, 2006; Goymann et al., 2004).

As field endocrinology techniques became established, experiments followed in which social interactions and hormone profiles were manipulated to determine cause and effect. A pioneering experiment by Harding and Follett (1979) on free-living red-winged blackbirds, *Agelaius phoeniceus*, showed that challenging males with a simulated intruder resulted in greater variability in total androgen (testosterone plus dihydrotestosterone, DHT) levels and the relationship of luteinizing hormone (LH) and DHT in experimental versus control males indicated that perhaps something was happening in response to social challenges. Interestingly, plasma levels of corticosterone were not affected by social challenge suggesting that social stress was probably not involved in suppressing LH and androgen secretion. These important results prompted us to measure corticosterone in future field experiments as a check that social stress was not a confound. Silverin (1980), working on natural populations of pied flycatchers, *Ficedula hypoleuca*, in Sweden was among the first to use subcutaneous implants of testosterone to change the normal temporal pattern. This study showed profound effects of altered testosterone pattern on male behavior, specifically reduced parental care, and lower reproductive success. These studies and many others to follow underscored how important it is to understand how individuals interact with their habitat, and with each other, and what implications there may be for hormone-behavior interactions and mechanisms.

Despite these exciting developments, one major issue that was looming for us was the perplexing and growing set of observations showing the wide variation in patterns of testosterone secretion and aggressive behavior across vertebrate taxa (Wingfield and Ramenofsky, 1985). One interpretation was that diverse patterns of testosterone profiles just represent inter-species variation and had no significance for cause and effect. Eventually it dawned on us that two major types of data on testosterone levels in relation to aggression in birds and mammals were evident. An analysis of many studies indicated that investigations failing to find any positive relationship of plasma testosterone and aggression in males were conducted in socially stable conditions. In contrast, those studies that did find a positive relationship of circulating testosterone levels and aggression were conducted during conditions of social instability such as when a new dominant male took over a group, or a male was challenged by another for its territory and mate (Wingfield and Ramenofsky, 1985). Work on primates such as rhesus macaques, *Macaca mulatta*, and later on olive baboons, *Papio anubis*, provided some key insights suggesting that experimental disruption of social hierarchies can affect sensitivity of neuroendocrine controls of the hypothalamo-pituitary axis by increasing or decreasing androgen secretion (Rose et al., 1975; Sapolsky, 1991). It was abundantly clear that observations and experimental manipulation of animals under natural conditions would be crucial to tease apart the complex and intriguing bases of hormone-behavior interactions during social instability in ecological contexts.

Beginning in 1981 at the Rockefeller University Field Research Station we had the opportunity and facilities to observe and sample free-living song sparrows and test whether social instability was indeed a driver of testosterone release. The results were very compelling and three field experiments showed that the effects of social instability in aggressive interactions among free-living males over territories and mates significantly elevated circulating testosterone levels compared with control males in more stable social conditions and not involved in aggressive interactions (summarized in Wingfield et al., 1990). There followed a flood of such investigations that opened up a new era of ecological studies and evolutionary insights into how neuroendocrine/endocrine control systems in social contexts arose. Our research group at Rockefeller (Gregory F. Ball, Alfred M. Dufty, Robert E. Hegner and Marilyn Ramenofsky) met weekly to discuss the growing evidence. Peter R. Marler, the Director of the Rockefeller University Field Research Center where all our early song sparrow work on the challenge hypothesis was conducted also provided key insight in terms of historical perspectives of "challenge" experiments. These lively discussions set the stage for the challenge hypothesis (Wingfield et al., 1990) which stated that:

1. Baseline levels of reproductive hormones such as LH and testosterone were involved in reproductive development and maintenance of the reproductive system throughout the breeding season.
2. The highly variable surges of LH and testosterone above the breeding baselines were correlated with territorial aggression and only occurred during social instability.
3. Male-male interactions over status and access to sexually receptive females tended to increase testosterone secretion.
4. Expression of paternal care and other "costs" required that testosterone secretion decrease.

We now had a framework to explain the complex temporal patterns of testosterone secretion, i.e. they reflect a "trade-off" of aggressive interactions and the degree of paternal care.

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