

BEHAVIOR

Hormones in the Middle

Ellen D. Ketterson

I first became interested in hormones and social behavior while conducting an experiment on birds in the field. My colleagues and I were studying the evolution of male parental care by comparing the reproductive success of two groups of female dark-eyed juncos (*Junco hyemalis*), those rearing young with the assistance of a male and those forced to rear young alone because we had captured their mates. We reasoned that any difference between the two groups could be attributed to the male's help, giving us a quantitative measure in numbers of offspring of what that help was worth. As it turned out, however, our experiment was not so simple. Removing males led to the appearance of "replacements" whose presence had not been anticipated but whose behavior proved fascinating. Some replacement males fed the female's offspring, while others chased and courted the females but ignored the offspring (1). I had to know what underlay these different male behaviors. Did an individual's experience of having been a parent in the past, or of having copulated with a particular female, make him more or less likely to care for his neighbor's young? If there were selective advantages to adopting, why did only some of the males adopt? Was parental behavior latent in all male birds owing to its early origin within the clade? And what was the role of hormones such as testosterone and prolactin?

In *Hormones and Animal Social Behavior*, Elizabeth Adkins-Regan addresses the roles played by hormones in the social life of animals. The author, a behavioral endocrinologist at Cornell University, aims her book at researchers who seek a greater understanding of behaviors whose profitability to the actor depends on how other animals respond. Social behavior includes fighting, mating, signaling, pair bonding, and parenting. Adkins-Regan explores how hormones connect variation in these behaviors to variation in fitness, life history, alternative phenotypes, sex, and evolution. In so doing, she takes the reader sledding from brain to behavior and from hormones to

gene expression, up and down through levels of analysis that often change within a single sentence.

Adkins-Regan's approach to hormones and behavior is one part common sense and one part rigor. The common sense is expressed in an informal writing style that sometimes makes you smile. For example, when she describes the ability of one individual's behavior to alter gene expression in another, she refers to the power of animals to "tickle each others' genomes." And when she summarizes the role of hormones in the development of insect castes in which an individual's caste develops not as dic-

tated by its genes but by its nutritional and social environment, she writes that "queens are made, not laid." The author couples her conversational style with insistence on the most rigorous standards for knowing. She frequently points out how confined our knowledge is by the small number of species studied and hammers home the point that it is not safe to assume that what is true for one species is true for another.

One of Adkins-Regan's many accomplishments in the book is her successful integration of Niko Tinbergen's celebrated four questions. Tinbergen was awarded a Nobel Prize for his seminal contributions to ethology, the most lasting of which may be the roadmap he provided for the study of animal behavior. According to Tinbergen (2), a full understanding of any behavior requires that we know how it develops, how it is mediated by underlying mechanisms, how it contributes to fitness, and how it evolved. Many have cited the importance of this approach, but to my mind Adkins-Regan is the first to have achieved a true synthesis, and she has done so by putting hormones front and, importantly, center. To oversimplify, the environment acts on the animal from the outside to stimulate hormone release, while

genes work from the inside to produce the enzymes that synthesize hormones and the receptor proteins that respond to them in target tissues. The hormone in the center stimulates or represses behaviors that influence fitness, causing the hormonal mechanisms that mediate behavior to evolve as social behavior evolves.

Deep understanding of the role of hormones in the expression and evolution of behavior is nevertheless challenging. In the relatively easy cases (for example, aggressive behavior in male chickens), you castrate and the behavior goes away; you provide hormone replacement, and the behavior comes back. More often, however, in the strictest sense hormones cannot be said to cause behavior, because the organism can produce the behavior in the absence of the hormone. That is, the behavior is "there" in the animal, and the hormone's role is to facilitate, mediate, coordinate, suppress, and otherwise alter the likelihood of the behavior's expression. Consequently,

Hormones and Animal Social Behavior

by Elizabeth Adkins-Regan

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Mating under the influence. In the rough-skinned newt (*Taricha granulosa*), the interactions of peptides and steroids lead males to mate in response to female stimuli except when a predator threatens.

hormones often rise in the circulation after a behavior is expressed, as a response to the cues from the environment that elicited the behavior. Hormones may thus function to prepare the organism for future encounters with these same cues. Relying on an expected correlation between past and future can spare the animal drawbacks of expressing a behavior like aggression when it is not called for. The immune system and the development of acquired immunity provide a good analogy.

The evanescence of hormones and their loose connection with behavior can be frustrating to ecological and evolutionary biologists who were drawn to hormones because of their association with fundamental questions in sexual selection: sex differences,

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exaggerated displays and ornaments, female choice, male-male aggression, and male parental care. Wattles and plumes are evidence that sexual selection has occurred and measuring them is a straightforward affair, but the hormonal systems that promote their development are less a fixed property on which selection can act. More often these systems are plastic or flexible attributes of an individual that respond to changes in the environment; to obtain meaningful results, the attributes must be measured in relation to those of other individuals with which the organism interacts.

Is there potential for selection on this kind of hormonally mediated trait? Certainly. Individuals vary in hormonal response to cues from the environment and in sensitivity to the hormones they produce. This nexus of sensitivity and response can be acted on by selection, giving rise to differences in aggression, bonding, and fighting. But as Adkins-Regan so clearly explains, we are just beginning to understand how. For example, we know very little about how different traits come to be regulated by the same hormone and even less about how they might escape such control. In well-studied cases like the links among testosterone, aggression, and parental behavior, the hormone is known to

facilitate the coexpression of adaptive characters to form suites or syndromes. Such hormonal pleiotropy can help to explain genetic correlations that cause characters to respond to selection in a coordinated way. But what happens when one or a few of these co-occurring correlated characters are no longer beneficial? How, in a mechanistic sense, are correlations broken and short-term constraints overcome? Answers are currently elusive, but the guideposts Adkins-Regan provides to young researchers should make them more attainable.

At least two practical applications of the perspective provided by the book broaden its appeal. First, it offers insight regarding how animals are likely to respond to climate change. Many seasonal organisms employ hormones to coordinate their breeding to the time when conditions in the environment are appropriate. The cues that trigger hormone secretion and behavioral and physiological response differ by species and sex, but in general they have proven to be reliable predictors over time. Alternative cues that are better predictors of the new realities brought by climate change will surely be available, and over time selection will favor those individuals that adjust the timing of their breeding. But the unit of selection may be the

coordinated hormonal responses of males and females, and such adjustments may take some time, whereas the rate of environmental change may be rather rapid. A second practical application concerns endocrine-disrupting chemicals in the environment, and here organisms may have less opportunity to adjust. Some of these chemicals hijack ancient and fundamental mechanisms that cannot be readily revamped. Although understanding hormonal mechanisms can again enhance predictions regarding outcomes, the ability of selection to fix the situation may be far more limited.

My only criticisms of Adkins-Regan's book are really requests for more. More illustrations would have been useful throughout, more extensive treatment of invertebrates and plants would have been welcome, and certain passages would have benefited from more citations. My overriding conclusion, however, is that *Hormones and Animal Social Behavior* is a highly illuminating book that is also a pleasure to read.

References

1. L. Wolf, E. D. Ketterson, V. Nolan Jr., *Anim. Behav.* **36**, 1601 (1988).
2. N. Tinbergen, *Z. Tierpsychol.* **20**, 410 (1963).

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ECONOMICS

Taxation with Representation

Thomas Piketty

Growing *Public* is an ambitious attempt to disentangle the complex interaction between social spending and economic growth in the developed countries since the 18th century. There is no doubt that Peter Lindert's book will have a long-lasting impact in the social sciences, both for its substantive conclusions and for its methodological contributions.

Over the past 30 years, Lindert (an economist and economic historian at the University of California, Davis) has published articles and reference books on long-running trends in income and wealth distribution in the United States and the United Kingdom and on the quantitative history of social spending. Drawing on his past work as well as an impressive array of archival material and new research, the author offers a fresh look at two old questions: Why did the uses of taxes for social programs evolve the way they did in Western Europe and North America over the past three cen-

turies? And what was the impact of such social spending on economic growth and development?

The author's key conclusion can be summarized as follows: modern welfare states are the fruit of democracy, not of bureaucracy, and democratic markets are basically efficient. According to Lindert, and contrary to a view commonly held (especially in the United States), this explains why the rise of social spending—from less than 1% of the gross domestic product (GDP) in the United Kingdom and the Netherlands in 1750 to over 30% of GDP in Nordic countries in 2000—has had no long-term negative impact on economic growth in these countries. Instead, the effect might even have been a positive one. In particular, Lindert persuasively demonstrates that countries with large welfare states have always been careful enough to finance their social spending using a distortion-minimizing tax mix. For instance, tax pro-

gressivity (the increase in average tax rates with increasing income) has typically been more modest in the Nordic countries than in the low-spending Anglo-American world. More generally, countries with large welfare

states have created substantial tax exemptions to encourage savings and capital accumulation. These countries have also relied extensively on proportional taxes on labor income (payroll taxes and social contributions) and consumption (especially of goods that are addictive, used in leisure activities, or threaten health or the environment, such as tobacco, alcohol, and gasoline). In addition, the structure of spending in the large welfare states has been

designed to minimize negative effects on productivity—for example, through an emphasis on public health and education or on pro-women and anti-old-age labor supply policies.

Lindert argues that this careful fine-tuning of the structure of taxes and spending in modern welfare states is not accidental. It is instead largely due to functional democracy: democratic political markets provide checks and balances that allow control of the costs of social spending. Lindert's emphasis

**Growing Public:
Social Spending and
Economic Growth Since
the Eighteenth Century**
by Peter H. Lindert

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Volume 2, Further Evidence

240 pp. \$75, £50. ISBN 0-521-82175-4.

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