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Symposium 14　Integrating mechanism and function in bird behavior: how hormones can help

Introduction

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1　Overview

Ever since Tinbergen, behavioral biologists have appreciated that a complete understanding of behavior will require knowledge of its function, causation, evolution, and development. In the past decade, each of these approaches has been highly successful, leading to development in behavioral ecology, behavioral physiology, developmental psychobiology, and comparative biology. However, the development of these subdisciplines has only enhanced the need to integrate proximate and ultimate approaches, a goal that has thus far proved elusive.

While answers to questions regarding the functional/evolutionary significance of behavior in birds are necessarily different from those about how behavior manifests itself within the lifetime of the individual, each approach can strongly benefit the other. Thus knowledge of problems faced by birds in the wild should guide questions posed about causal mechanisms, while knowledge of the limitations and plasticity in causal mechanisms should guide questions posed about the function and evolution of behavior.

This symposium focused on how studies of hormones can help to integrate different levels of analysis of bird behavior and physiology. Hormones are key to understanding behavior at the proximate level because they influence many aspects of the behavioral and physiological phenotype that are important functionally. For example, they act early in development to set a course, interact with other physiological systems such as the immune system, coordinate the expression of secondary sex characteristics, reflect the environment in the stress response and metabolism, and serve to coordinate the timing of reproduction. Hormones are also key to understanding how secondary sex characteristics evolve and how life history evolution can be constrained by trade-offs. Further, they move across generations as maternal effects and so influence phenotypic development in future generations much as genes do. Their effects on behavior, moreover, enable species-specific adaptations to match social systems to their environments.

2　Review of papers presented

In reporting their own hormonal studies, the speakers at this symposium provided outstanding examples of the power of an integrative approach, as follows.

2.1　Integrating steroid synthesis with steroid action

Schlinger, Soma and London summarize fascinating new alternatives to the traditional view of how gonadally derived sex steroids influence expression and development of sexually differentiated behaviors in birds. In particular, they focus on two well studied examples: the roles of testosterone in activating male territorial behavior and estradiol in organizing the vocal control system of oscine songbirds. In recent years, territorial aggression during the non-breeding season was found to be unresponsive to castration but still dependent on sex-steroids in song sparrows. Further, the song system in male zebra finches was found to develop in male castrates and not to develop in females induced to grow testicular tissue. The prevailing paradigm, which asserted that gonadal steroids enter systemic circulation to take effect in brain, often after conversion to estradiol, could not accommodate these findings.

Thanks to the work of Schlinger et al., we may be approaching resolution. They provide evidence that the adrenals secrete a precursor to testosterone and estradiol, DHEA, that circulates and has its effect on aggression in the brain without some of the “pleiotropic effects” we normally attribute to testosterone (e.g., reduced immune function or elevated metabolism). With respect to the song system, estradiol that is produced *de novo* in the brain from cholesterol may have its masculinizing effect *in situ*. These new findings add great depth to our knowledge of how steroids induce behavior without altering our fundamental understanding of steroids as activators of gene expression and determinants of sex differences.

Concerning adaptation and constraint in the evolutionary process, the findings suggest a mechanistic means by which constraints can be overcome. If complex phenotypic characters that evolved under one proximate mechanism can be handed off to another and accomplished with fewer costs (e.g., territorial aggression in the non-breeding season without suppressed immunity), then constraints in the form of physiological trade-offs provide less of a barrier to evolution because the trade-offs themselves are dynamic and change with the seasons.

The findings on sexual differentiation in the song system also help to explain how complex phenotypes of many characters can evolve. By coupling and uncoupling their dependence on systemic steroids, tissues can develop and evolve as modules. One of the most-studied sex differences in birds is copulatory behavior, one that obviously requires close coordination between brain and gonad: if you make sperm, then mount; if you make eggs, then squat. But, as the authors point out, vocal behavior has no necessary connection to gametogenesis, and lineages in which vocal behavior and copulatory behavior are free to evolve independently in males and females have apparently been favored — at least that appears to be the case for the zebra finch. Both types of behavior remain dependent on the same steroid to activate gene expression, but copulatory behavior is plugged into the systemic circulation, while song is freestanding. Only further research will uncover new examples and extend our understanding of how hormone-dependent characters evolve.

2.2 Hormones, sexual dimorphism and mate choice

Elizabeth Adkins-Regan summarizes the important developmental and organizational role played by steroid hormones in producing traits shaped by selection that is natural (with respect to reproduction) and sexual (with respect to successful acquisition of mates). By altering the levels of hormones very early in life, she sex-reversed three attributes: mounting partners in copulation, production of song to attract partners, and opposite-sex partner preference. This indicates that natural steroids establish male-typical or female-typical behaviors.

In quail, natural ovarian estrogens lead to female-typical behavior. Blocking the estrogens leads instead to male-typical behavior, including copulatory mounting and interest in females. If, in zebra finches, genetic females are treated with estradiol when young, they will behave like males by singing and preferring females. This work reveals the epigenetic power of steroid hormones in the organization of the phenotype. By affecting the expression of genes that are usually sex-specific in expression, and thus silent in the other sex, steroid hormones can induce maleness in females or femaleness in males.

Adkins-Regan's fascinating and compelling work on partner preference is especially interesting and raises many new questions: what aspect of typical females appeals to masculinized females and makes them more attractive than typical males? Is it their behavior? Or their silence? Are naturally more masculine females ordinarily attracted to naturally less masculine males as in, for example, the white-throated sparrow?

Her work stresses that attributes which typify one sex can be expressed as modules able to evolve separately. By relying on steroids for organization, including brain-derived steroids that require several enzymatic conversions for synthesis, evolution could favor individuals in which one site in the brain is masculinized or feminized early in development by conversion of a circulating steroid at the site, while another site is left unorganized because it did not express the converting enzyme. Much remains to be learned about how sexual dimorphism evolves, but comparisons of the role of organization in ancestral and derived species that differ in the degree of dimorphism are sure to be informative.

Adkins-Regan also links this research to Reeve and Spellman-Reeve's protected invasion theory, in which the mode of chromosomal sex determination explains why male birds may have evolved to be more dimorphic than male mammals. In birds, males are the homogametic sex, and mutant alleles arising on the Z chromosome would be less likely to be lost when new and rare because they would be present in both sexes. In their model, such protection of rare alleles permits retention of novel forms long enough for them to increase via sexual selection. Organizational actions extend this protection to steroid regulated genes on autosomes.

Much remains to be learned. Almost all that we know about the organizational effects of steroidal hormones on sexual preference, song, and mounting has come from studies of a just a few species, and interesting differences are apparent. Imagine how much more will be learned about these important and fascinating processes as researchers turn to new study systems and employ new tools (see paper by Schlinger et al.).

2.3 Hormone, brain, immune interactions and song

Ball, Duffy, and Gentner assess singing by male European starlings and its impact on females. Their studies exemplify a productive blend of proximate and ultimate explanations for bird behavior. Male starlings sing their songs in bouts, and bout length varies among males. Those singing longer bouts have enlarged vocal control regions in the brain and are preferred by females. The neural basis for the preference is not known, but Ball et al. have shown that immediate early gene expression in the auditory forebrain is greater in females exposed to longer bouts of song. If we were to assume that the variation among males in song and among females in preference had a genetic basis, we would expect selection to favor males that sing longer bouts unless there were balancing costs. If instead variation among males in song is attributable to environmental variation that allows some males to devote more resources to song, we might predict cost-free success for the longer-bout males, but no response to selection.

The results fit neatly with the balancing costs hypothesis. Males that sing longer bouts also have higher levels of plasma testosterone, and males with higher testosterone respond less robustly to immune challenges, suggesting costs to attractiveness. However, Ball et al. show that males which sing longer bouts have more robust immune responses to immune challenges. This apparently contradictory finding may be explained by assuming that only good quality males can afford to become attractive by producing high levels of androgens and bearing the costs of immune suppression. Such correlations between hormone, behavior and physiology hold great promise for future studies of selection on correlated characters mediated by hormones; they also pose challenges for those seeking to understand links between health and attractiveness.

2.4 Additional papers

Two other presentations in this symposium addressed the importance of testosterone, each from rarely studied perspectives. Groothuis et al reviewed the wide array of effects, both beneficial and costly, of androgen production in young birds, and described several ways in which the chicks can reduce these costs. Further, they showed how parents can adjust androgen production in their chicks to the level needed for social competition via choice of a nest site, so affecting the social context in which young are reared. In the other paper, Sandell et al. reviewed the importance of androgen production in female birds and placed the results in an evolutionary context. They asked whether testosterone in females has similar or different effects to that in males. This is an intriguing question because if testosterone affects similar traits in both sexes, but with beneficial effects in males and detrimental ones in females, the latter may constrain the evolution of testosterone production and its effects in males. These two papers (S14-2 and S14-4) were read as orals and only submitted as abstracts already published in the Abstract Volume of the Congress; they are not repeated here.