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Review article

Endocrine and neuroendocrine regulation of fathering behavior in birds

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ABSTRACT

This article is part of a Special Issue "Parental Care".

Although paternal care is generally rare among vertebrates, care of eggs and young by male birds is extremely common and may take on a variety of forms across species. Thus, birds provide ample opportunities for investigating both the evolution of and the proximate mechanisms underpinning diverse aspects of fathering behavior. However, significant gaps remain in our understanding of the endocrine and neuroendocrine influences on paternal care in this vertebrate group. In this review, I focus on proximate mechanisms of paternal care in birds. I place an emphasis on specific hormones that vary predictably and/or unpredictably during the parental phase in both captive and wild birds: prolactin and progesterone are generally assumed to enhance paternal care, whereas testosterone and corticosterone are commonly—though not always correctly—assumed to inhibit paternal care. In addition, because endocrine secretions are not the sole mechanistic influence on paternal behavior, I also explore potential roles for certain neuropeptide systems (specifically the oxytocin–vasopressin nonapeptides and gonadotropin inhibitory hormone) and social and experiential factors in influencing paternal behavior in birds. Ultimately, mechanistic control of fathering behavior in birds is complex, and I suggest specific avenues for future research with the goal of narrowing gaps in our understanding of this complexity. Such avenues include (1) experimental studies that carefully consider not only endocrine and neuroendocrine mechanisms of paternal behavior, but also the ecology, phylogenetic history, and social context of focal species; (2) investigations that focus on individual variation in both hormonal and behavioral responses during the parental phase; (3) studies that investigate mechanisms of maternal and paternal care independently, rather than assuming that the mechanistic foundations of care are similar between the sexes; (4) expansion of work on interactions of the neuroendocrine system and fathering behavior to a wider array of paternal behaviors and taxa (e.g., currently, studies of the interactions of testosterone and paternal care largely focus on songbirds, whereas studies of the interactions of corticosterone, prolactin, and paternal care in times of stress focus primarily on seabirds); and (5) more deliberate study of exceptions to commonly held assumptions about hormone–paternal behavior interactions (such as the prevailing assumptions that elevations in androgens and glucocorticoids are universally disruptive to paternal care). Ultimately, investigations that take an intentionally integrative approach to understanding the social, evolutionary, and physiological influences on fathering behavior will make great strides toward refining our understanding of the complex nature by which paternal behavior in birds is regulated.

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Introduction

Paternal care, or care provided by males that is directed at eggs or young, is more common among birds than any other vertebrate class. Biparental care is exhibited in more than 80% of avian species (Cockburn, 2006; Kendeigh, 1952), and rearing of altricial young (which generally requires significant parental input in the form of warming, protection, and feeding before chicks the nest) occurs in more than 70% of avian species (Silver et al., 1985).

Birds are strictly oviparous; thus, with the exception of egg-laying, male birds are generally capable of participating in the same range of parental behaviors as females. Such behaviors include indirect care such as nest building and feeding females during incubation, or more direct care including incubating eggs, assisting with hatching, brooding young, feeding young or escorting them to feeding sites, guarding eggs and chicks, and tidying the nest (Ketterson and Nolan, 1994; Silver et al., 1985; Vleck and Vleck, 2011). The extent to which males contribute to care of eggs and young also varies widely across avian species. Some males provide no care of eggs or young, some share parental care duties with females, and far fewer provide exclusive care of young (reviewed in Cockburn, 2006; Ketterson and Nolan, 1994; Silver et al., 1985). Thus, collectively, birds represent an excellent taxon for not only investigating the evolution of paternal care in vertebrates, but also for investigating proximate mechanisms underpinning diverse aspects of male care of young across a variety of contexts (e.g., Ball, 1991; Ketterson and Nolan, 1994).

Existing studies of the endocrine bases of paternal care have focused largely on circulating hormones (especially testosterone and prolactin), with a strong early emphasis on captive males in a laboratory setting (e.g., Buntin, 1996). This work has been instrumental in guiding our investigation of the proximate mechanisms of paternal behavior. As studies of paternal care have been extended to free-living birds, we have begun to develop a clearer understanding of how ecology and life history might shape the relationships between endocrine and neuroendocrine secretions and fathering behavior. Even so, much of what we know is rooted in correlational studies. Thus, despite paternal behavior being so common among birds, surprisingly little is known about the diversity of endocrine and neuroendocrine mechanisms governing fathering behavior in this vertebrate group.

Importantly, though male care is widespread in birds, it is not always essential for survival of young—females of many biparental species appear able to compensate for reduced or absent care by males, at least in the short term (e.g., Dunn and Hannon, 1992; Freeman-Gallant, 1998; Gowaty, 1983; Smith et al., 1982; Whillans and Falls, 1990). This suggests that endocrine and neuroendocrine mechanisms of paternal behavior may be shaped by considerably different selective pressures than mechanisms of maternal behavior. Even so, a large number of studies of paternal care have been conducted in biparental species, where shared care of eggs and young includes expression of common behaviors by males and females. Thus, one may be tempted to assume that mechanisms governing "parental behavior" in birds are also common between the sexes. However, emerging work indicates that mechanisms of male and female parenting behavior are not always the same (possibly due to sexual dimorphisms in neural substrates, receptor distributions, and circulating hormone profiles). Thus, a need exists for a clearer understanding of how fathering and mothering behavior are differentially regulated in birds, even when behavioral expression seems very similar.

Here, I review much of what is currently known about proximate mechanisms of paternal care in birds. Though this review does not provide an exhaustive treatment of the subject, I emphasize specific hormones that vary predictably and/or unpredictably during the parental phase in both captive and wild birds, and that thus are likely candidates for regulating fathering behavior. Some of these hormones (i.e., prolactin and progesterone) are generally assumed to enhance paternal care and others (i.e., testosterone and corticosterone) are commonly—though not always correctly—assumed to inhibit paternal care. I also highlight studies in which investigators have considered the dynamics of multiple hormones simultaneously (e.g., the interrelationships of corticosterone, prolactin, and fathering behavior in times of stress), and summarize key findings that suggest a potential role for specific neuropeptides in promoting paternal care in birds. In particular, I focus on the vasopressin–oxytocin nonapeptides, which are known to promote aspects of parental care in mammals, and gonadotropin inhibitory hormone, which interacts in key ways with hormones known to affect fathering behavior, such as testosterone and corticosterone. In addition, because endocrine secretions are not the sole mechanistic influence on paternal behavior, I touch on how certain experiential factors such as prior experience and feedback from offspring and mates might influence fathering behavior in birds. Throughout this review, I not only distill what is currently known about selected endocrine and neuroendocrine mechanisms governing fathering behavior in birds, but I also highlight areas that are ripe for future study.

Testosterone and fathering behavior: does testosterone mediate a conflict between sexual/territorial and paternal behavior?

Circulating testosterone during the parental phase

Seasonal activation of the hypothalamo-pituitary-gonadal (HPG) axis leads to elevations in testosterone in anticipation of breeding in seasonally breeding birds. In males, this elevation is important for seasonal development of some secondary sex characters, spermatogenesis, sexual behavior, mate attraction and territory defense during breeding (Balthazart, 1983; Wingfield et al., 2000; Wingfield and Farner, 1993). Testosterone is also commonly considered to be a potent inhibitor of paternal care, at least in certain contexts (Ketterson et al., 1992; Lynn, 2008; Wingfield et al., 1990).