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Review

The value of comparative approaches to our understanding of puberty as illustrated by investigations in birds and reptiles

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ABSTRACT

This article is part of a Special Issue "Puberty and Adolescence".

Studies of birds and reptiles have provided many basic insights into the neuroendocrine control of reproductive processes. This research has elucidated mechanisms regulating both early development, including sexual differentiation, and adult neuroendocrine function and behavior. However, phenomena associated with the transition into sexual maturation (puberty) have not been a focus of investigators working on species in these taxonomic classes. Research is complicated in birds and reptiles by a variety of factors, including what can be extended times to maturation, the need to reach particular body size regardless of age, and environmental conditions that can support or inhibit endocrine responses. However, careful selection of model systems, particularly those with available genetic tools, will lead to important comparative studies that can elucidate both generalizability and diversity of mechanisms regulating the onset of reproductive maturity.

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Introduction: sexual maturation in birds and reptiles

Puberty refers to the physiological processes by which an individual attains sexual maturity and is thus able to reproduce successfully as an adult. As such, it is a key component of the general process of development. Developmental biology has a long and distinguished history of employing a wide range of species in order to understand the complex sequence of events that underlies how a zygote is transformed into an adult (Wolper and Tickle, 2010). Curiously, although all vertebrate species go through some process to attain sexual maturity, scientists who study non-mammalian vertebrates generally have not made puberty a major focus of their investigations. Thus, while substantial data are available from a comparative perspective on early brain development of, and adult plasticity in,brain and behavior, this critical phase of maturation is under-investigated.

A common pattern is that experiments completed on the physiology of puberty in non-traditional organisms have come from investigators interested in the control of reproductive cycles. As has been noted by several of these scholars (e.g., Foster et al., 1986; Nicholls et al., 1988), the study of seasonal breeding involving an individual cycling between

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states of being reproductively active or inactive is a potentially powerful model to gain insights into puberty. This developmental stage involves processes that control the transition from being a juvenile that is reproductively inactive to a reproductively functional adult, a process that is to a large degree recapitulated in seasonally breeding adults. Comparative studies of neuroendocrine control of seasonal reproduction have thus been one important source of insight into the physiology of puberty. However, it is not clear whether the mechanisms are fully parallel across these processes or whether the first instance of reproductive competence differs in terms of mechanism or function. In this review, we briefly summarize the current state of knowledge about puberty in birds and reptiles, and will offer some general ideas about the potential value of comparative studies on this topic.

The development of sexual maturity in birds

There are approximately 10,000 extant species of birds present on earth today (Clements, 2007). Nearly 50% of these are members of the order Passeriformes (songbirds; Clements, 2007). Passeriformes typically reach sexual maturity within one year. In temperate zone species this would mean that a nestling hatched in the late spring or summer would either migrate or overwinter and then be capable of breeding the following spring. This sort of pattern or some variant (depending on when breeding occurs and whether the species is highly seasonal) is the most common pattern of puberty among avian species (Follett, 1991). Some species, especially those that live in highly variable habitats such as the Australian outback will reach sexual maturity in less than one year. The zebra finch (*Taeniopygia guttata*) and other estrildid finches are an example of such a pattern of puberty. In larger long-lived species such as member of the Charadriformes (i.e. gulls and terns), the Procellariformes (fulmars, petrals and albatrosses), the Pelicaniformes (i.e., gannets, boobies and frigatebirds) or the Cinconiiformes (i.e., storks) the attainment of sexual maturity can be delayed two, three years or even more (Diomedia albatrosses usually require 7 years for example). These patterns encompass pubertal patterns exhibited by the vast majority of avian species. A consideration of what is known about the neuroendocrine basis of these patterns will form the focus of this section on puberty in birds.

What is the pattern of sexual development in birds that mature within their first year of life?

In seasonally breeding birds, the annual cycle of reproductive and non-reproductive activity can in many species be characterized by understanding how the birds' transition among three different physiological states that are defined based on their responsiveness to seasonal variation in photoperiod (Dawson et al., 2001; Nicholls et al., 1988). Lessons learned from the annual cycle of adults are then applied to thinking about the development of a mature reproductive state in juvenile birds. This strategy has been applied in most detail to European starlings (*Sturnus vulgaris*; Follett, 1991). Adult starlings in late fall and winter have regressed reproductive systems (i.e., small gonads and negligible concentration of sex steroid hormones in the blood). Long days in the late spring and early summer stimulate rapid reproductive growth and put the birds in a state of photostimulation. Other factors then act to fine tune the exact timing of breeding. Long days also set into motion another process that leads to the regression of the reproductive system so that the birds stop breeding before food supplies decline and there are no sufficient resources to feed their progeny. This state is known as 'photorefractoriness'. Starlings that are photorefractory will not respond with appropriate reproductive growth to any daylength including constant light. The photorefractory state is usually dissipated over the course of the fall by the experience of short days. Short days essentially re-set the hypothalamo-pituitary–gonadal (HPG) axis so that the starlings are ready to respond to long days again. Birds that have experienced short days and are ready to respond to long days are said to be photosensitive.

Starlings hatch in the summer when daylengths are long but they do not respond to these with any sign of reproductive development (McNaughton et al., 1992; Williams et al., 1987). It was hypothesized that starlings were born in a photorefractory state and then experienced short days in the fall of their first year which rendered them photosensitive and allowed them to respond to long days and experience sexual maturity during the spring of their first year of life (Farner et al., 1983). A series of clever experiments involving raising young starlings (even while in the egg!) on short days showed that that is indeed the case (McNaughton et al., 1992; Williams et al., 1987). Starlings will start to respond to short days only after they reach adult size at 21 days after hatch. If placed on short days at this time they will start the process of breaking this juvenile photorefractoriness and exhibit changes in reproductive physiology characteristic of sexual maturity as early as day 21 or 28 after that (McNaughton et al., 1992). However, prior to day 21 of life they will not respond to short days. It is not because they are insensitive to daylength; studies of the timing of their pattern of molt indicate that these birds can indeed respond to daylength (McNaughton et al., 1992). The reproductive axis is unable to respond to daylength and therefore exhibit sexual maturity. What is the nature of this deficit? Is it a simple lack of development?

Studies relevant to this question have recently been completed in Japanese quail, a photoperiodic species that breeds after less than one year of life year. These studies investigated the ontogeny of neurons that migrate to the preoptic area (POA) a critical brain area for the control of the HPG axis and reproductive behavior. In contrast to starlings, the young in quail is precocial. The ontogeny of new neurons is largely complete in quail by embryonic day 16, but new neurons are incorporated in a second wave at the onset of sexual maturity in the first spring of life (Mouriec et al., 2011). This second wave that occurs in association with the onset of puberty and the activation of sexual behavior and may be one cellular marker of essential changes needed for puberty to commence.

What is the pattern of sexual development in birds that mature in substantially less time than one year?

Some avian species breed in an opportunistic manner (Hahn et al., 2008). Opportunistic in this case, refers to the fact that some critical resources are unpredictable and species that rely on them respond with a rapid increase in reproductive physiological activity when these resources become available. Species exhibiting this pattern for the organization of reproductive activity can be contrasted with seasonally breeding species that generally track highly predictable resources such as the availability of a food source that emerges every year in a reliable fashion (Wingfield, 2008). One of the most intensively studied opportunistic species is the zebra finch (Zann, 1996). This species lives in the harsh Australian outback and can only breed when the environment improves in response to increases in rainfall. Developing zebra finches can reach sexual maturity within 60 to 120 days depending on their sex and the specific environmental conditions when they are born and develop (Zann, 1996). The development of the HPG axis has not been investigated in detail but once these birds reach sexual maturity they tend to maintain the reproductive neuroendocrine system in a tonically elevated state (Hahn et al., 2008). One possibility is that puberty occurs once the birds develop sufficiently for their HPG axis to be functional. However, this hypothesis would need to be investigated carefully. A related issue is whether "opportunistic" species that occur in diverse taxa and diverse habitats all exhibit a similar pattern of sexual development (Hahn et al., 2008).