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The evolution of photoperiod response systems and seasonal GnRH plasticity in birds

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Synopsis Animals' lives are typically subdivided into distinct stages, some of which (e.g. breeding) contribute to fitness through enhancing current reproductive success, and some of which (e.g. molting and migration in birds; hibernation in mammals) contribute to fitness through enhancing survival and, therefore, future reproductive opportunities. There is often a trade-off between these two kinds of processes, either because they are temporally incompatible with one another (e.g. migration precludes simultaneous nesting in birds) or because they are energetically incompatible with one another (e.g. successful molting appears to be incompatible with simultaneous nesting in many birds). Consequently, adaptations facilitating appropriate timing and coordination of different life-cycle stages are arguably as important to fitness as more obvious adaptations such as feeding morphologies and predator avoidance. Mechanisms that facilitate coordination of life-cycle events with the annual cycle of changes in the environment are therefore expected to evolve in response to selection imposed by different environmental challenges. This article focuses on how mechanisms affecting the timing of, and transitions between, life-cycle stages, particularly breeding, have evolved in birds. Through comparative analyses, we show that photorefractoriness and one neuroendocrine correlate of it—plasticity of the gonadotropin releasing hormone system—have evolved in ways that facilitate different degrees of flexibility in timing of the transition from breeding to molting in different environments. We argue that the nature of the mechanistic adaptations will affect the capacity for adaptive adjustments to changing environmental conditions both in the short term (plasticity inherent in individuals) and in the long term (evolutionary responses of populations to selection).

Introduction

Most of our planet exhibits cyclical changes in weather and resources, and as a result many organisms organize their annual cycle such that offspring are produced when resources are abundant, and other life-history stages occur at other times. Seasonally breeding temperate-zone birds often reproduce in the spring coincident with the peak abundance of invertebrates that they feed their young. They then molt their feathers in the late summer or autumn, and are reproductively quiescent over winter. Since the pioneering work of Rowan (1925, 1926) a plethora of research has demonstrated that the annual change in photoperiod is used as a proximate cue by many birds to organize their annual cycle, including the onset and termination of reproduction and migration (Dawson et al. 2001; Wingfield and Farner 1993).

A large body of work on seasonally breeding songbirds such as house finches (*Carpodacus mexicanus*), European starlings (*Sturnus vulgaris*), white-crowned sparrows (*Zonotrichia leucophrys*), juncos (*Junco hyemalis*), and others, has revealed a general pattern of photoperiodism (Fig. 1) (Dawson 2003; Dawson et al. 2001). In the winter birds experience a relatively short photophase and long scotophase ("short day" photoperiod). During this time birds are reproductively quiescent, but can respond to increases in the photophase; at this time they are said to be "photosensitive". As spring approaches and the hours of daylight increase beyond a certain length two processes are initiated. First, birds are "photostimulated," and increase release of gonadotropin-releasing hormone (GnRH) and gonadotropins that stimulate gonadal growth, increased secretion of sex steroids, and eventually

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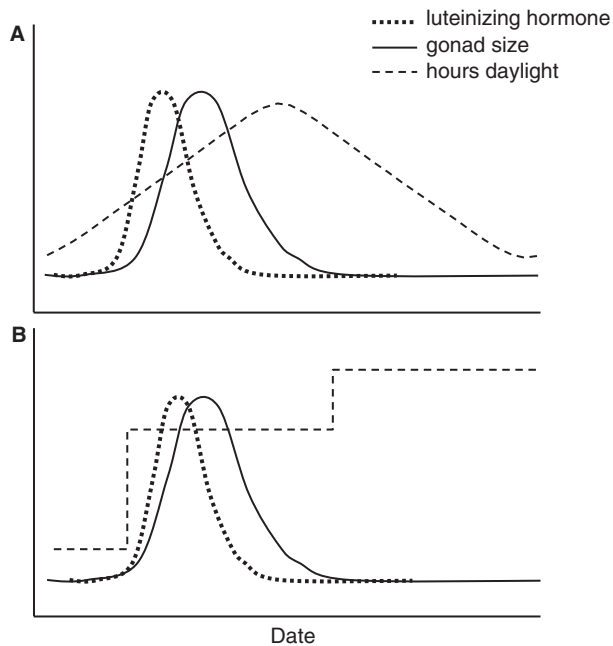


Fig. 1 Photoperiodism in seasonally breeding songbirds. **(A)** Under natural photoperiods, lengthening days in spring result in photostimulation: a surge in gonadotropin release followed by gonadal growth. Eventually the birds become photorefractory, insensitive to the stimulatory effects of long days, and the gonads regress. **(B)** In a controlled environment the two criteria for absolute photorefractoriness can be demonstrated. Criterion 1: The gonads spontaneously regress while the birds are exposed to constant long days. Criterion 2: Lengthening the photoperiod has no effect on the gonads once photorefractoriness has been established.

reproduction. Second, following a delay of several weeks the exposure to long days results in the eventual onset of “photorefractoriness” (Nicholls et al. 1988). During photorefractoriness, photophases that were previously long enough to stimulate gonadal recrudescence cease to be stimulatory, GnRH declines, and the reproductive system collapses leading to eventual gonadal involution. In many species, the onset of photorefractoriness and regression of the gonads are followed by prebasic molt and migratory fattening.

Photoperiodism and GnRH plasticity

In seasonally breeding songbirds, the annual cycle is organized through cyclical transition between the states of photosensitivity, photostimulation, and photorefractoriness. Photorefractoriness terminates reproduction during summer, presumably allowing time to complete molt before the onset of inclement conditions. In songbirds, photorefractoriness has typically been identified as “absolute photorefractoriness.” Absolute photorefractoriness has been

operationally defined by two criteria (Fig. 1B). First, the gonads regress and molt ensues with no decrease in the length of the photophase—criterion 1. This may involve regression of the gonads prior to the summer solstice, or following extended exposure to a constant long-day photoperiod in the laboratory (Nicholls et al. 1998). Second, once photorefractoriness is established it is absolute in that exposure to even longer duration photophases (24 h light in the extreme) do not lead to gonadal recrudescence (Hamner 1968; Nicholls et al. 1988)—criterion 2. When they are photorefractory, birds also appear to be refractory to all previously stimulatory environmental cues, not just to photoperiod (Ball 1993; Goodson et al. 2005; Dawson and Sharp 2007).

Absolute photorefractoriness is associated with a profound decrease in the hypothalamic content of GnRH in a number of songbird species—the annual decline in reproductive function is associated with reduction in the amount of GnRH-I protein in the hypothalamus (e.g. Dawson et al. 1985; Foster et al. 1987; Goldsmith et al. 1989; Parry et al. 1997). Recently, the gene for songbird GnRH-I has been identified in European starlings (Stevenson et al. 2009) and zebra finches (*Taeniopygia guttata*, Ubuka et al. 2009). Hypothalamic GnRH-I mRNA expression is up-regulated at sexual maturation (Ubuka et al. 2009) and also varies as a result of photoperiodic condition (Stevenson et al. 2009). Seasonal GnRH plasticity is observed in both free-living birds (e.g. Cho et al. 1998; Marsh et al. 2002), and in birds with extended exposure to constant long days in the laboratory (e.g. Dawson et al. 1985; Foster et al. 1987). Moreover, seasonal changes in GnRH have been reported for two forms of GnRH: GnRH-I and GnRH-II (Stevenson et al. 2005). Although GnRH down-regulation is associated with photorefractoriness, it does not appear to be the cause. Instead, down-regulation of GnRH likely follows the onset of photorefractoriness rather than precedes it, as substantial GnRH immunoreactivity is present in the hypothalamus of white-crowned sparrows during the early stages of photorefractoriness (Meddle et al. 2006). Moreover, treatment with *N*-methyl-*D*-aspartate can result in elevation of gonadotropins in white-crowned sparrows that are photorefractory but not yet deeply so (Meddle et al. 1999). These results suggest that development of photorefractoriness first involves cessation of GnRH release, which is then followed by a gradual cessation of GnRH synthesis (Dawson et al. 2001; Dawson and Sharp 2007; Stevenson et al. 2009).

Interspecific diversity

The pattern of absolute photorefractoriness and GnRH plasticity described above can be contrasted with other forms of photoperiodism in birds. Japanese quail do not become absolutely photorefractory, but instead exhibit “relative photorefractoriness.” Unlike absolute photorefractoriness by criterion 1, relative refractoriness requires a decline in photoperiod for its expression (Robinson and Follett 1982), or a decline in multiple environmental cues (Wada et al. 1990; Wada 1993). Unlike absolute photorefractoriness by criterion 2, exposure to longer photophases can reinstate reproductive competence following the onset of relative photorefractoriness (Robinson and Follett 1982). GnRH plasticity in quail is negligible (Foster et al. 1988; Follett and Pearce-Kelly 1990; Teruyama and Beck 2000).

Prior to the past decade, it appeared that photoperiodism involved absolute photorefractoriness and seasonal GnRH plasticity in songbirds on the one hand, and relative photorefractoriness without seasonal GnRH plasticity in a non-songbird, Japanese quail, on the other. Since that time, however, data on a greater number of species have revealed a complex distribution across species of birds in the two criteria for absolute photorefractoriness and GnRH plasticity (Dawson and Sharp 2007; Hahn and MacDougall-Shackleton 2008). Opportunistically breeding songbirds may never become refractory. For example, red crossbills held on constant long days for over 300 days failed to regress their gonads, thus failing to exhibit criterion 1 of absolute photorefractoriness (Hahn, 1995). Crossbills also show only very modest seasonal changes in GnRH immunoreactivity (MacDougall-Shackleton et al. 2001; Pereyra et al. 2005).

We surveyed the literature for information on photoperiodism and GnRH plasticity in birds to address the following questions. How does the nature of photorefractoriness vary among species? How does GnRH plasticity vary among species? How might selection modify photoperiod response systems in response to selection for diverse breeding schedules?

Absolute photorefractoriness criterion 1

The majority of seasonally breeding songbirds studied to date spontaneously regress their gonads after extended exposure to long days. Of 40 or so songbird species for which data have been reported, only four taxa failed to exhibit this form of photorefractoriness

(Hahn and MacDougall-Shackleton 2008; Hahn et al. 2009). Expanding the comparison to include all species of birds for which we have found data, only three additional species do not exhibit this form of photorefractoriness (Fig. 2). The distribution of species that do not spontaneously regress their gonads suggests that this is a derived trait in each group, and has evolved multiple times independently. Indeed, the most parsimonious conclusion, given the data we have, is that the dinosaur-like last common ancestor of all birds was probably photoperiodic, and spontaneously regressed its gonads while on long days. This tentative conclusion would be strengthened, however, if further data were available from a greater number of tropical species. The bias toward temperate-zone species in the literature may bias our interpretation of the phylogenetic history of photoperiodism in birds.

The breeding schedules of the birds that fail to regress their gonads without declining day length support the hypothesis that in some taxa photorefractoriness by criterion 1 has been selectively lost as an adaptive specialization (Hahn and MacDougall-Shackleton 2008). Crossbills and zebra finches are opportunistic breeders; crossbills can breed through about 10 months of the year, and zebra finches regularly breed in all months at some locations (Hahn et al. 2008). Rufous-winged sparrows (*Aimophila carpalis*) breed flexibly depending on the time of monsoon rains (Small et al. 2007), and other *Aimophila* sparrows also appear to not regress their gonads spontaneously (Deviche and Small 2005). Subtropical rufous-collared sparrows (*Zonotrichia capensis*) have extended and flexible breeding seasons, and wood pigeons (*Columba palumbus*) have very long breeding seasons facilitated by the fact that they feed young on crop milk. The remaining two species that do not exhibit criterion-1 photorefractoriness have been selectively bred through domestication for continuous reproduction. Thus, the presence, and absence, of criterion-1 photorefractoriness appears well associated with breeding schedule.

Absolute photorefractoriness criterion 2

There are fewer species that have been tested for the second criterion of absolute photorefractoriness (Table 1). Japanese quail do not become absolutely photorefractory by either criterion. Among the 22 species of songbirds for which data are available, only five do not exhibit absolute photorefractoriness by criterion 2. That is, only a few species are able to

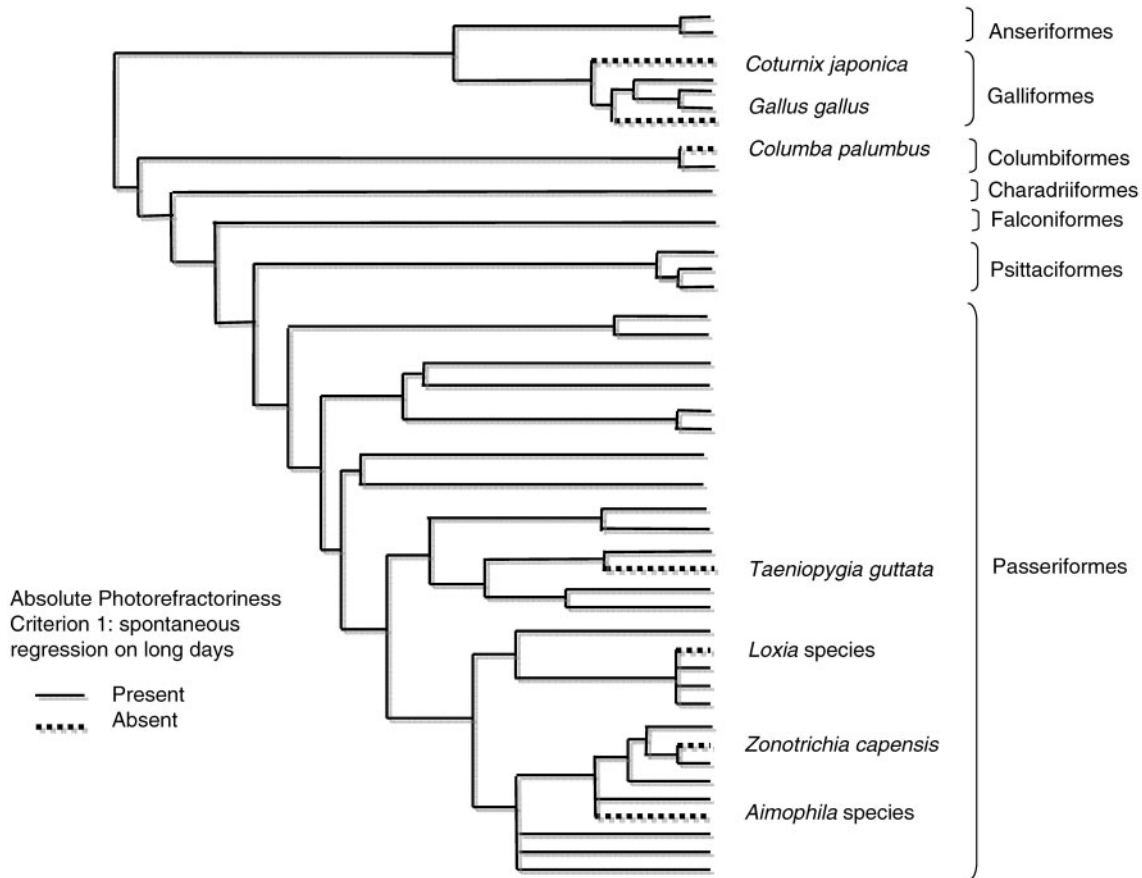


Fig. 2 Distribution of absolute photorefractoriness, criterion 1, among birds. Data from Hahn and MacDougall-Shackleton (2008) and Hahn et al. (2009). Phylogeny adapted from Sibley and Ahlquist (1990), based on DNA–DNA hybridization.

respond to very long days once photorefractoriness and regression of the gonads has begun. These include tropical antbirds (*Hylophylax naevioides*), opportunistically breeding crossbills, and flexibly breeding *Aimophila* sparrows. The ability to respond to long days during photorefractoriness is also present in several cardueline finches in addition to the crossbills: American goldfinches that breed seasonally but relatively late in the year, pine siskins that have a long and flexible breeding season, and gray-crowned rosy-finches that have a short breeding season at high elevations and latitudes.

Data are available for too few species to draw strong conclusions regarding the evolutionary history of this form of photorefractoriness. Among songbirds, complete insensitivity to long days while photorefractory is widespread and may be ancestral. However, the most basal songbird for which we have data (spotted antbirds) does not exhibit this trait. In addition, domestic Japanese quail become only relatively refractory and do not exhibit this trait. Clarifying the evolutionary history of criterion-2 absolute photorefractoriness will require data from

a broader range of species. Indeed, it is unclear whether the relative rarity of a lack of criterion-2 photorefractoriness is a result of it being a less common trait, or a result of opportunistic breeders being understudied.

A lack of insensitivity to cues is present in some opportunistic and flexibly breeding species, consistent with the idea that loss of the trait is an adaptive specialization for opportunistic or flexible breeding. However, this trait is also absent in some seasonally breeding species such as American goldfinches and gray-crowned rosy-finches. Further undermining the idea that the distribution of criterion 2 reflects adaptive specialization is the observation that criteria 1 and 2 are usually, but not always, concordant within species (Fig. 3). Pine siskins spontaneously regress their gonads on long days (criterion 1), but are not insensitive to very long days when photorefractory (criterion 2) (Table 1). This observation indicates that the two criteria for absolute photorefractoriness are not interchangeable, and may reflect different mechanisms that contribute to the photoperiod response system.

Table 1 Species of birds that have been tested for absolute photorefractoriness criterion 2 (complete insensitivity to cues when refractory)

Common name	Latin name	Refractory	Conditions/comments	Citation
Japanese quail	<i>Coturnix japonica</i>	No	16L:8D	Robinson and Follett (1982)
Blossomheaded parakeet	<i>Psittacula cyanocephala</i>	Yes	22L:2D	Maitra (1987)
Spotted antbird	<i>Hylophylax naevioides</i>	No	22L:2D, 13L:11D	Beebe et al. (2005)
European starling	<i>Sturnus vulgaris</i>	Yes	16L:8D	Burger (1947)
Brahminy myna	<i>Sturnus pagodarum</i>	Yes	16L:8D, 24L:0D	Kumar and Kumar (1991)
Black-capped chickadee	<i>Parus (Poecile) atricapillus</i>	Yes	24L:0D	Phillmore et al. (2005)
Garden warbler	<i>Sylvia borin</i>	Yes	15L:9D	Gwinner et al. (1988)
House sparrow	<i>Passer domesticus</i>	Yes	18L:6D	Dawson (1991)
common (Baya) weaver	<i>Ploceus philippinus</i>	Yes	16L:8D	Bisht and Chandola-Saklani (1992)
Red crossbill	<i>Loxia curvirostra</i>	No	24L:0D	MacDougall-Shackleton et al. (2006)
Pine siskin	<i>Carduelis pinus</i>	No	24L:0D	MacDougall-Shackleton et al. (2006)
Canary	<i>Serinus canaria</i>	Yes	~15L:9D, ~18L:6D, 20L:4D	Kobayashi (1957)
House finch	<i>Carpodacus mexicanus</i>	Yes	24L:0D	Hamner (1968)
Cassin's finch	<i>Carpodacus cassinii</i>	Yes	24L:0D	MacDougall-Shackleton et al. (2006)
Common/scarlet Rosefinch	<i>Carpodacus erythrinus</i>	Yes	24L:0D	Tewary and Dixit (1983)
gray-crowned rosy-finch	<i>Leucosticte tephrocotis</i>	No	24L:0D	MacDougall-Shackleton et al. (2006)
White-throated sparrow	<i>Zonotrichia albicollis</i>	Yes	20L:4D	Wolfson (1958)
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	Yes	15L:9D	Farner and Mewaldt (1955)
Golden-crowned sparrow	<i>Zonotrichia atricapilla</i>	Yes	15.5L:8.5D	Miller (1951)
Dark-eyed junco	<i>Junco hyemalis</i>	Yes	20L:4D	Wolfson (1952)
American tree sparrow	<i>Spizella arborea</i>	Yes	24L:0D	Wilson and Reinert (1996)
Rufous-winged sparrow	<i>Aimophila carpalis</i>	No	16L:8D	Small et al. (2007)
Rufous-crowned sparrow ^a	<i>Aimophila ruficeps</i>	No	16L:8D	Deviche et al. (2008)
Cassin's sparrow ^a	<i>Aimophila cassinii</i>	No	16L:8D	Deviche et al. (2008)
Black-headed bunting	<i>Emberiza melanocephala</i>	Yes	23L:1D	Pratima Devi and Lai (1994)
Bobolink	<i>Dolichonyx oryzivorus</i>	Yes	14L:10D; based on beak pigmentation	Engels (1962)

Unless otherwise noted the response measured was gonadal growth in response to increased photophase.

^aData for *Aimophila ruficeps* and *A. cassinii* are consistent with a lack of criterion-2 photorefractoriness, but further experiments are required to fully demonstrate this.

GnRH plasticity

Data on GnRH plasticity are limited to Japanese quail and relatively few species of songbirds (Fig. 3). A lack of seasonal down-regulation of GnRH is present in opportunistically breeding crossbills and zebra finches, and continuously breeding Japanese quail (reviewed by Hahn et al. 2009). Although GnRH down-regulation is absent in one domestic strain of canaries, American singers (Bentley et al. 2003), it is present in another strain, border canaries (Hurley et al. 2008). In white-crowned sparrows, GnRH is clearly present during the early stages of photorefractoriness (reviewed above), but is likely down-regulated when birds are

deeply photorefractory as injection of hypothalamic extracts from such birds fails to induce gonadotropin release (Wingfield and Farner 1993). Thus, among seasonally breeding species, corresponding GnRH down-regulation seems to be widespread regardless of the length and flexibility of the breeding season. This is consistent with the idea that year-round maintenance of GnRH is an adaptive specialization in species with opportunistic breeding.

It makes intuitive sense that maintenance of GnRH year-round would facilitate opportunistic breeding by allowing rapid transduction of stimulatory environmental cues into a neuroendocrine signal. The comparative data, however, are not in clear support of this idea. First, the clearest

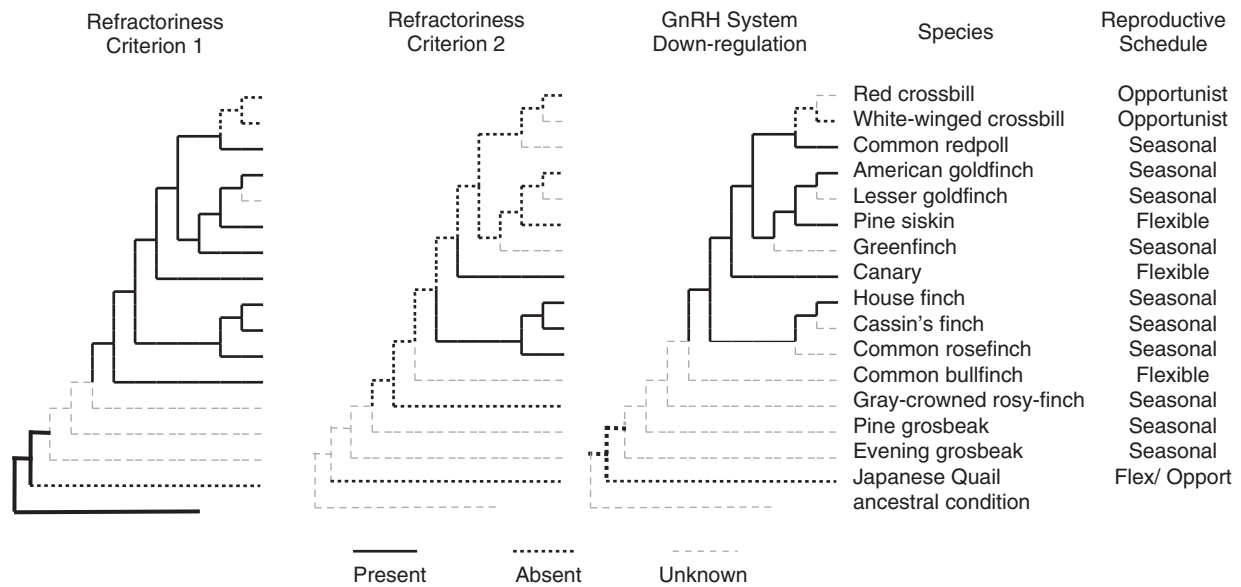


Fig. 3 The distribution of absolute photorefractoriness, criteria 1 and 2, and GnRH flexibility among cardueline finches, Japanese quail (as an outgroup), and the likely common ancestral condition. Data compiled by MacDougall-Shackleton and Hahn (2008). Phylogeny adapted from Marten and Johnson (1986), Badyaev (1997), and Arnaiz-Villena et al. (2001).

relationship between photoperiod responses and opportunistic or flexible breeding is with criterion 1, not criterion 2. That is, there is a closer association between opportunistic/flexible breeding and the failure to spontaneously regress the gonads than to remain sensitive to photoperiod while photorefractory (see above). Despite this, maintenance of GnRH year-round is more closely associated with a lack of both criteria 1 and 2 as compared to those that lack only criterion 1 (Fig. 3). Second, some species, such as pine siskins, do down-regulate GnRH but are still able to rapidly respond to very long days even when putatively photorefractory (Fig. 3; MacDougall-Shackleton et al. 2006), suggesting an ability to reverse GnRH down-regulation rapidly.

Cryptic flexibility and photoperiod responses

The lack of concordance between criteria 1 and 2 of absolute photorefractoriness highlights the importance of considering multiple components of photoperiodic response systems. For any given species, there are a number of different parameters that contribute to photoperiodic responses. These include, among many others, the required length of photophase to initiate gonadal recrudescence in the spring, the nature of photorefractoriness, and whether or not short days are required to break photorefractoriness and reinstate photosensitivity

(reviewed by Hahn et al. 1997; Hahn and MacDougall-Shackleton 2008). For at least the two criteria of absolute photorefractoriness, these parameters can evolve independently in different species (Fig. 3).

In addition, these results highlight the fact that many aspects of photoperiodic response systems may not be apparent in the wild, and require testing the parameters of the system under controlled conditions. As recently noted, it is important to consider both field and laboratory experimental data to understand complex biological systems (Calisi and Bentley 2009). Among cardueline finches, in particular, we have identified several species that have a more flexible response system than would be predicted by their breeding schedule (MacDougall-Shackleton et al. 2006). Gray-crowned rosy-finches are high-elevation specialists or high-latitude specialists and have very short breeding seasons. Yet, they retain the ability to respond to long days even when putatively photorefractory. Molting birds that were exposed to 24 h light rapidly arrested molt and showed substantial testicular growth within 10 days (MacDougall-Shackleton et al. 2006). It is unclear whether this responsiveness is an adaptation allowing this species to fine-tune their short breeding season in a harsh environment, or whether it simply reflects phylogenetic history. The presence of responsiveness in this relatively basal cardueline lineage suggests that this trait may represent a preadaptation of the cardueline finches that has resulted in their diversity

of breeding schedules (MacDougall-Shackleton and Hahn, 2007; Hahn and MacDougall-Shackleton, 2008).

Data on GnRH plasticity are not available for rosy-finches, but pine siskins do down-regulate GnRH following prolonged exposure to constant long days (Pereyra et al. 2005). Despite this, they, like rosy-finches, are able to respond to very long days after regressing their gonads (MacDougall-Shackleton et al. 2006). It is counter-intuitive that a species that has down-regulated GnRH to the point where there is very little immunoreactivity would be able to rapidly grow their gonads in response to long days. However, there is growing evidence that GnRH synthesis and release can be modified very rapidly in response to a variety of cues. In birds, both GnRH-I and GnRH-II are modulated by social cues (Mantei et al. 2008; Stevenson et al. 2008). In musk shrews, GnRH-II is modulated by energy balance and by social factors (Kauffman and Rissman 2004; Temple et al. 2003). In anurans and fish, GnRH neurons can change in response to changes in the social environment (Burmeister and Wilczynski 2005; White et al. 2002), potentially on very rapid time scales (Burmeister et al. 2005). Thus, at least some species of birds may retain the ability to rapidly up-regulate GnRH synthesis and release in response to some environmental cues, even when photorefractory by criterion 1.

The evolution of photoperiod response systems

As noted above, for any given species the photoperiod response system has several different features. The day length required to induce gonadal recrudescence in the spring may vary from species to species. The delay from the onset of photostimulation to the onset of photorefractoriness most likely also varies. Selection on the first of these parameters could result in a species advancing its breeding season in the spring in response to favorable conditions. Selection on the second could result in an extended breeding season. By modifying a few such parameters it is potentially possible to modify a photoperiod response system that would produce a strictly seasonal breeding schedule into one that is almost entirely opportunistic (Hahn et al. 2009). Because these different parameters of photoperiod response systems are dissociable, it seems likely that selection acting differentially on these mechanisms could give rise to the diversity of photoperiodic responses and breeding schedules observed among birds.

In modeling how photoperiod response systems may evolve, it is important to note that each parameter of the system exhibits phenotypic plasticity. That is, each parameter's effect on the phenotype will depend on the environment, and as such will need to be characterized as a reaction norm. The photoperiod response system, being comprised of several such parameters, would thus be characterized as a multi-dimensional reaction norm.

Implications

Our comparative review of photoperiod response systems of birds reveals that the many parameters that make up such systems are dissociable. Previously we have described at least 13 photoperiod response parameters that are potentially susceptible to natural selection (Hahn and MacDougall-Shackleton 2008). Above, we review two of these: the two criteria of absolute photorefractoriness. Although these two criteria were once thought synonymous it is now clear that they are distinct and likely have separate physiological mechanisms. Many other photoperiod response parameters are also likely to be distinct and separable. One value of comparative approaches is that they highlight variation in these parameters and can provide direction for future research into mechanisms.

The parameters of photoperiod response systems are phenotypically plastic. They are phenotypically plastic in the traditional sense, in that environmental variation during development modifies the trait in the adult (for example, Coppack et al. 2001). However, photoperiod response systems are also conditionally plastic in adulthood. That is, the nature of the photoperiodic response depends, in part, on the nature of the change in photoperiod (MacDougall-Shackleton and Hahn 2007). The same species breeding at different latitudes can exhibit different patterns of breeding phenology stemming from the same photoperiod response system. Thus, photoperiod response systems will be very complex to model, but require a reaction norm approach (Nussey et al. 2007). Reaction norms will likely depend on current and developmental experience for each of the many parameters that comprise the system. However, characterization of all these parameters will be required to fully understand the flexibility and capacity of these response systems.

Understanding the capacity of avian photoperiod response systems is critical to an understanding of birds' abilities to cope with global change (Visser 2008). Individual birds have conditional plasticity,

and thus some capacity to respond to environmental change within their lifetime. In addition, different taxa have differing response systems, and the capacity of these systems may not be apparent from studies of free-living birds, such as the cryptic flexibility apparent in some cardueline finches. Phenotypic plasticity in the timing of reproduction can itself be under selection (Nussey et al. 2005). Thus, the potential reproductive flexibility of a species, or population, and its ability (or not) to cope with change requires characterization of the capacity of the system. For example, the capacity of great tits (*Parus major*) to track advancing peaks in abundance of food is limited by the plasticity of their responses to environmental cues (Visser et al. 1998; 2006). Understanding which populations are at risk requires characterizing their cue-response systems' capacity for flexibility. Understanding how individual birds cope with environmental variation similarly requires characterizing the mechanisms by which birds transduce variation in environmental cues to time their annual cycles.

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