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Seasonal timing and population divergence: when to breed, when to migrate

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Understanding how populations adapt to constantly changing environments requires approaches drawn from integrative and evolutionary biology as well as population ecology. Timing of reproduction and migration reflect seasonal pulses in resources, are driven by day length, and are also responsive to environmental cues that change with climate. Researchers focusing on birds have discovered accelerated breeding, reductions in migration, and extensive variation in perception, transduction, and response to the environment. We consider situations in which individuals experience the same environment but differ in the timing of the annual cycle. Such scenarios provide exceptional opportunities to study mechanisms related to among-population differences in timing (allochrony) and distribution (sympatry–allopatry–heteropatry), which have the potential either to enhance or reduce population divergence and biodiversity.

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Introduction

The urgency of environmental change coupled with the availability of new technology is transforming our understanding of phenomena that have fascinated biologists for generations: changing seasons, seasonal shifts in behavior and morphology, and remarkable feats of migration. The last decade has seen an explosion of studies into seasonal timing that seek to identify how changing climates are altering the biology of seasonally breeding organisms [1]. Emerging patterns in avian populations throughout the northern hemisphere include earlier breeding for many but not all species [1–3]. Migratory timing by birds has also been affected by warming [2,4–6]. Some species have shortened their migrations or ceased migrating altogether [4,7]. A related but distinct body of research has sought to elucidate the role of timing in phenotypic and genetic divergence *among populations* (see Table 1). Theoretical and empirical studies continue to challenge the view that speciation requires geographic isolation, and one focus has been to consider circumstances under which timing differences (allochrony) can give rise to reproductive isolation [8]. Studies of birds, plants, insects, fish, and bats have revealed among-population differences in timing that are interrupting gene flow, potentially leading to speciation [8–12].

Seasonal timing and population divergence

This contribution addresses how *seasonality in the environment and timing of events of the annual cycle relate to population divergence* by focusing on mechanisms of reproductive and migratory timing in birds. Working from the premise that selection acts on mechanisms that vary among individuals and populations and employing concepts and methods from three subfields, seasonality, evolutionary endocrinology, and geographic variation/population divergence, we briefly summarize what is new in the timing of reproduction and migratory biology as learned from intensive and prolonged study of individual bird species in the wild and in captivity.

Variation in timing within and among populations

It is almost a truism that members of a population experiencing the same environment will nevertheless differ among themselves in when they reproduce. Despite exposure to nearly identical day length, food supply, temperature, moisture, etc., some individuals breed early and some breed later. While some of this variation can surely be attributed to age or condition, individuals are also known to be consistently early or late owing to their underlying biological timing.

The existence of this individual variation presents an outstanding opportunity to study mechanisms mediating timing and how they respond to selection. Early and late breeders can be compared for response to a particular day length, patterns of gene expression, sequence differences in candidate genes, systemic variation in perception–transduction–response to environmental cues [13], and

Table 1

Recent studies of avian systems addressing integration of timing and population divergence by employing measurements of gene expression, endocrine correlates of reproductive and migratory behavior, selection gradients, sequence variation in candidate genes, geographic variation in genetic structure and in timing, and variation in urban versus wildland populations.

Study system	Approaches/references
Great tits *Parus major*	• **Gene expression** differences among populations that differ in **latitude**, following photoperiod treatment [63] • **Candidate genes** in relation to timing of breeding within a population, including **selection analysis**[a] [64] • **Longitudinal studies of selection** on **endocrine correlates** of timing of breeding within a population [65] • Divergence in timing of breeding among **urban versus wildland** populations in relation to artificial light [66]
Great and Blue Tits	• Integration of **candidate gene** and **quantitative genetic** approaches [67]
Blue tits *Cyanistes caeruleus*	• **Candidate genes** for timing of breeding *within*-pops. and *among*-pops. across **latitude** [68,69] • **Endocrine correlates** of timing among closely related populations inhabiting different **localized climates** • **Longitudinal studies of selection** on timing of breeding within and among populations [70] • Divergence in timing among **urban versus wildland** populations in relation to artificial lighting [66]
European blackbirds *Turdus merula*	• **Common garden** studies of timing of breeding and migration (*Zugunruhe*), including **endocrine correlates** in **urban versus wildland** populations [71–74] • **Loss of migration** and **neutral genetic divergence** among multiple **urban versus wildand** populations [75] • **Candidate genes** for timing and others traits among multiple **urban versus wildland** population pairs[a] [76] • Divergence among **urban versus wildland** populations in timing in relation to artificial lighting [66]
Blackcaps *Sylvia atricapilla*	• **Candidate genes** for migratory distances among (and within) populations [77] • **Artificial selection** (disruptive), leading to loss of migratory propensity [4] • **Ecological mechanisms** (eco-morphology) in relation to divergence in migratory populations across **latitude** [78] • Divergence in timing of (migratory) arrival and breeding phenology among sympatric cohorts, including analyses of **neutral genetic divergence** [79,80]
Barn swallows *Hirundo rustica*	• Analysis of **neutral genetic divergence** among variably migratory populations across **latitude/longitude** [11] • **Candidate (Clock) genes** in relation to timing of breeding, migration, life-history and molt, within and among populations, including **longitudinal studies of selection** [81,82] • **Loss of migratory** behavior (shifts northwards) in relation to climatic warming [83]
Dark-eyed junco *Junco hyemalis*	• **Endocrine correlates** of divergence in timing of breeding in **urban versus wildland** populations also inhabiting distinct **localized climates**, including **common garden** studies [84,85[•]] • **Loss of migration** in an **urban versus wildand** populations, including **common garden** approach (*Zugunruhe*) • **Candidate genes** for migratory distance *within*-populations and *among*-populations across **latitude** and **urban versus wildland**[a] [86] • **Common garden** for timing of breeding across **latitude**, incl. **endocrine correlates** in seasonal sympatry [87] • **Gene expression** in relation to divergence in timing and migratory strategy across latitude and urban versus wildland[b]
White-crowned sparrow *Zonotrichia leucophrys*	• Divergence in reproductive timing, migratory strategies, and life-history among closely related populations and subspecies, including **endocrine correlates** of divergence [88,89] [c] • Experimental studies of seasonal **gene expression** in relation to altered photoperiod and hormonal conditions [90]
Pied Flycatcher *Ficedula hypoleuca*	• **Longitudinal studies of selection** on **candidate genes** and **neutral genetic divergence** *within* and *among* populations across **latitude/longitude** [91[•]] • **Candidate genes** (Clock, ADCYAP1) in relation to timing of migration among individuals during migration [92] [a]
Florida scrub-jay *Aphelocoma coerulescens*	• **Endocrine correlates** in relation to divergence in timing among **urban versus wildland** populations, including evaluation of **ecological mechanisms** [93]

Table 1 (*Continued***)**

Study system	Approaches/references
Rufous-collared sparrows *Zonotrichia capensis*	• Divergence in timing (asynchrony) and **neutral genetic divergence** among two adjacent equatorial populations inhabiting different **localized climates** [94], including studies of **endocrine correlates**
Stonechats *Saxicola* spp.	• **Common garden** for timing of breeding and migration (*Zugunruhe*) among populations across **latitude** [95] • **Cross-breeding** to evaluate fitness consequences of reproductive timing in 'hybrid' pairs [95,96]
Seabirds	• **Neutral genetic divergence** and timing of breeding differences *within* and *among* island populations in sympatry [12] • **Ecological mechanisms** (habitat specialization, non-breeding segregation) underlying allochrony in sympatry [97] • **Ecological mechanisms** (energetics) in relation to divergent migratory strategy and allochrony under sympatry [98]

[a] These studies chiefly report negative results (i.e. lack of associations).
[b] Current research in progress by A. Fudickar *et al.*
[c] Also see ongoing research by M. Ramenofsky and Z. Németh.

fitness consequences of early and late reproduction. The same environmental cue might be stimulatory for some individuals and not for others at a different life-history stage and a critical question is why. In mice, individual variation in circadian rhythms was recently found to relate to distinct expression patterns of a key 'clock' gene, *PER2*, within the suprachiasmatic nucleus, the 'master circadian oscillator' [14]. It is probable that endogenous circadian rhythms influence seasonal photoperiodic timing decisions. Thus individual variation in timing mechanisms and responses to environmental cues may be influenced by photoperiodic history, history with other cues [14,15] and by genetic inheritance [16].

These comparisons can also be made across populations of the same species that differ in timing of reproduction. High latitude or high altitude populations, for example, often breed later, providing natural comparisons. Interpretation of these comparisons is challenging, however, because so many factors may contribute to differences observed. Spring may come later at higher latitudes, but obviously so many other aspects of ecology differ as well.

Species consisting of sedentary and migratory populations that co-exist for portions of the year make it possible to study the mechanisms underlying timing of reproduction and migration. Cross-population comparisons of systemic physiology and gene expression in organisms experiencing the same environment become accessible. Such situations also make it possible to examine how within-population variation might alter gene flow and give rise to among-population variation and thus population divergence.

Kevin Winker applied the term heteropatry to capture situations of 'seasonal sympatry, seasonal allopatry,' in which migrants and residents winter together in sympatry, but owing to the departure of migrants, breed in allopatry [1,17]. In such cases, residents typically initiate reproduction while migrants are still present, creating opportunities for hybridization that may or may not be realized. An important question is how such differences in timing in the same environment affect the likelihood of gene flow between migrants and residents. Do migrants mate with residents and give rise to ill-adapted young or do differences in timing prevent hybridization?

Timing of reproduction and migration and biodiversity

Comparisons of migrant and sedentary forms of the same species also raise the question of how migration-induced allopatry will respond to climate change and influence biodiversity. Future changes in animal movements may alter current patterns of overlap. If the tendency to migrate declines, such that currently allopatric breeding populations become sympatric, then opportunities for gene flow between migrant and sedentary forms may increase, leading to the merging of incipient species [18] and resulting in loss of nascent biodiversity. In other situations climate warming may lead to longer not shorter migrations, for example by migrants that currently breed at high altitudes. Finding favorable conditions for breeding that are currently achieved by flying uphill in spring may require a northward shift in latitude before breeding. Conversely, if formerly migratory forms become resident in portions of the breeding range from which they used to retreat, then populations that were sympatric in winter may now become allopatric year-round, reducing gene flow, reinforcing population divergence, and enhancing diversity. Combined study of mechanisms of timing, changes in animal movements, and niche modeling will contribute to predictions of the impact of environmental change on biodiversity.

We turn now to selected advances related to determinants of when to breed and when to migrate as they bear on how *seasonality in the environment and timing of the events of the annual cycle relate to population divergence.*

When to breed?

Multiple reviews of selective consequences of within-population variation in timing have appeared recently [19–21]. In some cases, researchers have shown that breeding is taking place earlier in warm springs, that earlier breeding is leading to higher reproductive success, and that breeding dates are heritable. Researchers are also addressing how mechanisms of response to the environment relate to phenological change [13,22,23]. Nevertheless, much remains to be learned about how mechanisms related to timing of reproduction vary among individuals and populations.

Onset of seasonal reproductive physiology and behavior has traditionally been studied as a response to seasonal changes in photoperiod (recently reviewed extensively [24••]), but photoperiod and other measures of the external environment (e.g. food, temperature, etc.) cannot account for how individuals and populations experiencing the same immediate environment exhibit variation in how they respond. Early and late breeders within a population, and heteropatric populations that overwinter together but breed separately are prime subjects for addressing internal mechanisms by asking where variation lies at the level of the organism, particularly where variation lies along the reproductive hypothalamo–pituitary–gonadal (HPG) axis.

One of many potential sources of within-population and among-population variation is the interaction between stress reactivity and onset of reproduction. We have long known that individuals vary in how they prepare for and respond to 'stressors' [25,26], and that stress can dampen the activity of the HPG axis [27]. Thus, a prime candidate accounting for within-population and among-population variation in timing is how stressors interact with the HPG during the critical window for timing decisions. Individuals with greater stress reactivity could be favored under certain environmental change scenarios, while individuals with lower stress reactivity could be favored under other scenarios [28]. Despite significant heritable variation in the avian stress response [29], all levels of the hypothalamo–pituitary–adrenal (HPA) axis can be altered during development, resulting in variations in adult phenotypes [30].

Resident bird species prepare for reproduction by altering the functioning of the HPA which releases corticosterone (CORT), a glucocorticoid that is one of the primary contributors to the stress response [31]. In house sparrows (*Passer domesticus*) glucocorticoid receptor (GR) expression varies seasonally and a recent paper showed that GR binding in the brain is at its highest in the pre-egg laying period, suggesting a greater sensitivity to CORT during this critical timing window [32].

Another way in which 'stress reactivity' may interact with the reproductive axis is via release and response to the neuropeptide, gonadotropin-inhibitory hormone (GnIH), which is expressed in the paraventricular nucleus (PVN) of the hypothalamus. GnIH is capable of down regulating activity of the HPG axis via binding with receptors on the pituitary, and, potentially, via direct influence on GnRH neurons in the hypothalamus (reviewed in [20]). GnIH cells possess glucocorticoid receptors, and treatment with CORT increases GnIH mRNA expression [33•]. Further, when norepinephrine, another signaling molecule that relates to stress, is injected into the PVN, quail increase *GnIH* mRNA transcription and GnIH release [34].

In addition to potential influence at the levels of the hypothalamus and pituitary, glucocorticoids may directly influence the ability of the gonads to respond to the gonadotropins produced by the pituitary [35]. Testes of photosensitive European starlings (*Sturnus vulgaris*) stimulated with LH/FSH *in vitro* increase testosterone production, but this production is significantly diminished if CORT is also administered [36•]. However, when administered to fully mature testes, CORT fails to decrease testosterone secretion when compared to administration with LH/FSH alone. Food restriction or limiting resources would be predicted to delay the onset of reproduction. Administration of the drug 2-deoxyglucose (2-DG), a glucose analog inhibiting glycolysis, thus inducing a metabolic 'stress,' has been shown to upregulate GnIH expression in the ovaries [36•], suggesting a way in which resource availability might influence timing of reproduction. These studies indicate that individual/population variation in 'stress reactivity' may be a strong target for investigations of how timing differences may arise in the same environment. In populations that migrate, reproduction is delayed until migration has been accomplished. Thus another key question that is still almost entirely unanswered is how the mechanisms that time reproduction interact with those mediating migration. One recent paper provides new evidence that the pathways are independent and may be subject to distinct regulation [37].

When to migrate?

Returning to our objective of how *seasonality in the environment and timing of the events of the annual cycle relate to population divergence*, we turn to new developments in migratory timing in birds where rapid advances are taking place owing to new technology.

Increasingly miniaturized geolocators, GPS loggers, satellite transmitters and other tracking devices deployed at breeding or wintering sites allow measurements of departure dates, migratory direction, duration and speed, and

destination of migrations (for review of tracking technology see [38]). Recent advances in methods for interpreting intrinsic markers, such as stable isotopes and genetic markers, are adding to our knowledge of how breeding and wintering ranges of migratory species are connected [39–42], including the recent application of large numbers of genomic (SNP) markers [43]. Additionally, carefully coordinated and standardized citizen-generated databases (e.g. Cornell's Feeder-Watch program) are providing invaluable information about the phenology and geography wild species in unprecedented ways [44,45].

An important challenge is to relate these increasingly precise measurements of migratory geography and phenology in the wild to the mechanisms that regulate timing. Monitoring (or manipulating) hormones before migration is fostering correlative and experimental approaches for exploring the regulation of migration [46,47,48•]. Further, studies of traditional measures of migratory readiness in caged migrants (fattening and nocturnal activity, referred to as migratory preparation) continue to be informative.

Recent studies investigating the links between early activation of the HPG in preparation for reproduction and migration have identified a role for testosterone in both. Experimental elevation of testosterone in captive migratory gray catbirds (*Dumetella carolinensis*) induced earlier spring migration [49], and early elevation of testosterone before departure supported both migratory and breeding preparation in free-living American Redstarts [48•]. However, testosterone alone is not sufficient for full expression of spring migration because castrated male white-crowned sparrows (*Zonotrichia leucophrys gambelii*) supplemented with testosterone fail to exhibit full migratory restlessness in spring [50].

Increased food consumption and nocturnal activity characterize migrant birds during the season of migration and have been associated with seasonal elevation in baseline levels of the adrenal steroid corticosterone (CORT) [51,52]. However the pattern is not consistent across all species [53], and experimentally altering the HPA has had inconsistent effects on migratory preparations [54,55].

Circulating levels of melatonin decrease in nocturnal migrants during the season of migration, suggesting that a reduction in melatonin may help to induce nocturnal activity [56,57]. However, experimental elevation of melatonin does not reduce nocturnal activity in migrating garden warblers (*Sylvia borin*) during stopover [58]. Individuals that had higher nighttime melatonin had greater diurnal activity and reduced body mass, indicating that nighttime melatonin [58].

Mechanisms as constraint

Reproduction and migration have traditionally been viewed as distinct stages with little to no overlap in time or neuroendocrine control mechanisms [21,59]. However, newer findings reveal that preparation for spring migration and reproduction overlap in time and are tightly linked in mechanism [49,50,60]. An issue of controversy is the degree to which one life-history stage (migration) imposes a constraint on the ability of the other (reproduction) to respond independently to selection. For example, recent studies monitoring changes in timing of spring migration and reproduction have found that as one advances in response to changes in climate, so does the other [6,61••], which is consistent with constraint. In White-crowned Sparrows exposed to green light during days that are long enough to stimulate gonadal growth if light is full spectrum exhibit migratory preparedness but not gonadal growth [37]. And a recent modeling paper [62], reports that variation among species in length of the breeding season and timing of pulses of resources needed for breeding predict circumstances under which migratory and reproductive timing can evolve independently and that existing data are consistent with the model's predictions. How reproductive and migratory timing respond to selection is fundamental to determining the role of timing (allochrony) in population divergence.

Conclusion

We conclude by referring the reader to Table 1, which contains a sampling of recent studies from 13 avian systems addressing integration of timing and population divergence. Collectively these studies serve as examples of what can be learned from examining the organismal and evolutionary mechanisms that facilitate population-level divergence in reproductive and migratory timing using a range of approaches including: measurements of gene expression, endocrine correlates of reproductive and migratory behavior, selection gradients, sequence variation in candidate genes, geographic variation in genetic structure and in timing, and comparisons of urban versus wildland populations. As systems are added and more methods are applied to already studied systems, the role of timing mechanisms in promoting or reducing gene flow and population divergence will become clearer. Areas particularly deserving of more study include the impact of timing mechanisms on mate preferences, the role of early developmental environments on the expression of migratory and reproductive timing in adults, and the interaction of mechanisms that time migration and reproduction. Ultimately predicting short and longer-term responses to environmental change will require greater knowledge of where variation in timing mechanisms currently resides among individuals and across populations. In time we will learn what changes when a migrant becomes a resident and vice versa, which will represent a major advance in our understanding of animal migrations.

Conflict of interest statement

Nothing declared.

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