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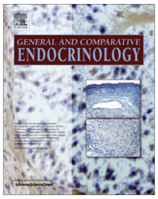

Review

# Contributions of endocrinology to the migration life history of birds

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ABSTRACT

Migration is a key life cycle stage in nearly 2000 species of birds and is a greatly appreciated phenomenon in both cultural and academic arenas. Despite a long research tradition concerning many aspects of migration, investigations of hormonal contributions to migratory physiology and behavior are more limited and represent a comparatively young research field. We review advances in our understanding of the hormonal mechanisms of migration with particular emphasis on the sub-stages of the migration life history: development, departure, flight and arrival. These sub-stages vary widely in their behavioral, ecological and physiological contexts and, as such, should be given appropriate individual consideration.

## 1. Introduction

Migration is an elegant example of the intimate relationship between organism and environment. Every spring incredible numbers of birds embark on flights for distant locations to take advantage of seasonally abundant resources in areas that are otherwise uninhabitable year-round. In autumn, migrants return to wintering grounds where resources are sufficient for overwinter survival and, eventually, for preparation to migrate to the breeding grounds again. In a show of remarkable phenotypic flexibility, migrants adjust their physiology and behavior as they pass through distinct stages of an annual schedule, which presumably maximizes fitness within seasonally predictable environments (Jacobs and Wingfield, 2000; Piersma and Van Gils, 2011; Ramenofsky and Wingfield, 2007).

Here we review the environmental and endocrine mechanisms that regulate specific components of the autumn and spring stages of migration. To address the regulatory mechanisms of migration, it is important to recognize that each of these stages is complex and composed of successive phases. First, the genetic, molecular and biochemical mechanisms underlying migration are initiated during the developmental phase. Following development, the mature expression phase includes cycles of fueling and flight. During fueling most migrants express hyperphagia (increased food intake) followed by fattening that includes lipogenesis in liver, storage in adipose tissue and deposition in flight muscle for the oxidative functions supporting long-distance flight (Jenni and Schaub, 2003; Jenni-Eiermann and Jenni, 1992; Marsh, 1984; McFarlan et al., 2009; Ramenofsky, 1990; Ramenofsky et al., 2011). Other organs also may change in size and activity as birds prepare for flights of variable duration, depending upon the migratory strategy. Departure involves the coordination of internal (e.g., fuel levels) and external (e.g., environmental) cues and, once in flight, many migrants will show oriented navigation and demonstrate remarkable metabolic and behavioral strategies to fuel long-distance flight (Guglielmo, 2010; Jenni-Eiermann et al., 2011). After completion of a fueling and flight cycle, migrants may stop to rest and refuel during stopover periods. Consecutive cycles of fueling and flight thus continue during mature expression until the destination is reached. Finally, transitions from the termination of migration to onset of the next stage entails a change from extended, oriented flight to a more facultative and, eventually, sedentary condition as breeding or over-wintering is initiated. Utilizing this refined framework, we begin our review with a model for environmental regulation of the spring and autumn stages of migration, which vary in ecological and physiological context. This is followed by in depth discussions of the endocrine mechanisms that regulate specific sub-stages of migration: fueling (hyperphagia and fattening), departure, flight, and arrival (termination of migration).

## 2. Environmental regulation of spring and autumn migrations

Clear distinctions exist between the spring and autumn stages of migration. For many overland migrants the spring and autumn stages cover nearly the same routes and individuals may express similar preparations for departure (Moore et al., 1985, 1982;

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Newton, 2008; O'Reilly and Wingfield, 1995; Ramenofsky, 2011; Wingfield et al., 1980). However, many facets of these stages differ. Environmental conditions including weather and daylength, orientation and navigation, reproductive state, speed of travel, intensity of fueling, available resources en route, as well as the age, sex ratio and flight experience of flock members can all differ between the two migrations and, presumably, exert different selective pressures on regulatory mechanisms. Fig. 1 presents a model of how environmental cues and physiological processes influence the onset and progression of the vernal and autumnal stages based on Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*), a north temperate overland migrant that uses one of the most common forms of migration (i.e., short bout, long-distance migration). Of course, many other migratory strategies exist with different consequences for regulatory mechanisms. For example, species that cross barriers en route (i.e., deserts, oceans, large massifs) will show less seasonal variation in the duration of migration or intensity of fueling than do typical overland migrants (Piersma and Van Gils, 2011). This emphasizes the significance of environmental factors in the evolution of migration and, presumably, its regulatory control.

Current understanding of the environmental and endocrine control of the two migratory stages has developed largely from studies of north temperate migrants, including species of *Fringilla*, *Parus*, *Zonotrichia*, *Junco*, *Spizella*, *Sturnus*, etc. (Dawson et al., 2001; Farner, 1959; Moore et al., 1982; Wingfield and Silverin, 2002; Wingfield and Farner, 1993; Wolfson, 1959). For these species, the initial predictive factor, or annual increase in photoperiod, serves as reliable information for timing of future seasonal events. It acts as a persistent cue or a "driver" promoting development of spring life cycle stages – pre-alternate molt, migration and, eventually, breeding (See Section 3 for more detailed information; (Moore et al., 1982; Ramenofsky and Wingfield, 2007; Wingfield and Farner, 1993). Furthermore, exposure to the long days of spring also influences autumnal stages. This largely occurs through the development of photorefractoriness: a condition that halts further reproductive activity through deactivation of the hypothalamic–pituitary–gonad axis and initiates pre-basic molt and autumn migration (Dawson et al., 2001; Moore et al., 1982; Nicholls et al., 1988). The influence of lengthening days on the development of photorefractoriness, however, acts remotely. Exposure to a prescribed number of days with greater than 12 h of light per day is required for the delayed expression of the linked or "internally coupled" post-breeding events (Moore et al., 1982). Captive Gambel's white-crowned sparrows held on photoperiods that are less than 12L fail to molt or exhibit autumn migratory features. Granted, such photoperiods do not occur in the field, but these results indicate that remote effects of photoperiod are acting in a directive capacity. The actual mechanisms regulating autumn migration are unknown, but environmental conditions certainly have an influence. In contrast to spring migration where increasing daylength acts as a driver, decreasing autumnal daylength tends to rush completion of pre-basic molt and preparation for departure from breeding grounds (Dawson et al., 2001; Moore et al., 1982).

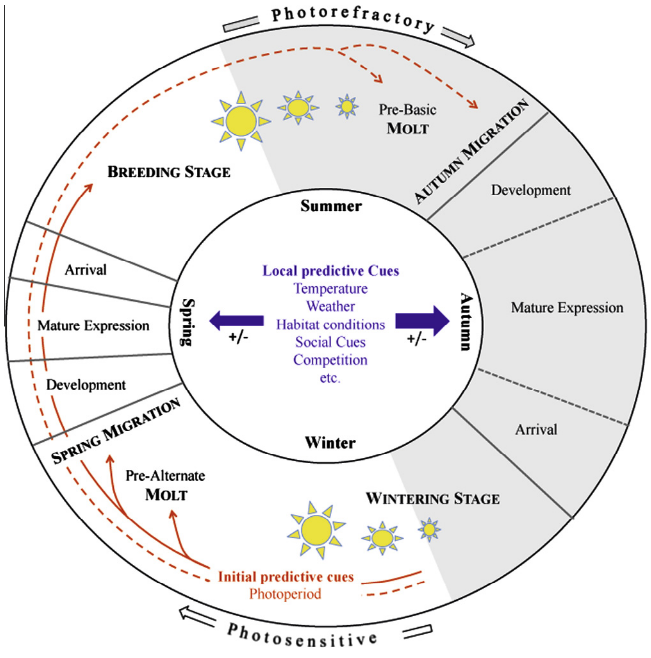

**Fig. 1.** Theoretical model of the effects of environmental conditions on spring and autumn stages of migration based on studies of north temperate overland migrants. Progression of the annual schedule is read in the clockwise direction. Initial predictive cues, in synergy with underlying endogenous rhythms, have direct/immediate effects (red solid lines) on photosensitive birds by inducing the onset of pre-alternate molt and progression of the spring migratory and reproductive functions. Exposure to increasing photoperiods in spring also has remote or delayed effects (red dashed lines) with the onset of photorefractoriness (shaded gray) that terminates breeding and induces onset of the postnuptial molt and progression of the autumn migratory functions. Local predictive cues (blue) provide more fine tuned information and affect the speed by which organisms move through the migratory stages. Sun icons of decreasing size (summer) and increasing size (winter) represent changes in the photoperiod after the respective solstices.

Patterns of change in daylength also vary by season and latitude. For birds that migrate to higher latitudes in the spring, the rate of change in daylength increases with northward movement. At the polar circles (66° 33′ 39 N or S) birds will experience continuous light from June 6 for nearly one month. In contrast, the rate of decreasing daylength in autumn is slower than the rate of increase in spring, particularly at high latitudes (King, 1963; Moore et al., 1982). These seasonal distinctions may contribute to the different mechanisms by which photoperiod affects spring and autumn migration. For example, north-temperate, trans-equatorial migrants face unique challenges because these species winter in the southern hemisphere, where they experience lengthening days that begin to shorten following the winter solstice. Such species seem to have evolved different responses to photoperiod to avoid developing a migratory disposition during the winter. For example, the bobolink (*Dolichonyx oryzivorus*) remains relatively refractory while migrating south and only regains photosensitivity in spring when a migratory disposition is appropriate (Hamner and Stocking, 1970).

The mechanisms by which photoperiod is perceived and transmitted for development of spring migration have been described as a system of photoreceptors and neuroendocrine pathways of the medial basal hypothalamus and the pineal gland (See Section 3 for review; (Kuenzel et al., 1999; McMillan, 1972; Stetson, 1971; Stetson and Erickson, 1972; Yokoyama, 1976). Recent studies of the regulation of the developmental phase of breeding identified photoreceptive cells at multiple sites throughout the brain (Foster et al., 1985; Wang, 2007; Wang and Wingfield, 2011; Yoshimura, 2006). Wang (2007), however, has suggested that the photoreceptors and photopigments that regulate onset of spring migration may differ from those of the breeding stage, indicating separate neuroendocrine pathways for the migration and breeding stages – a point raised earlier (Stetson, 1971; Stetson and Erickson, 1972). Whether the regulatory sites for autumn and spring migration are also different remains an open and intriguing question. Wilson (Wilson, 1989) suggested the linkage of autumn migration with photorefractoriness and molt may indicate that this is the case.

Endogenous rhythms are also important in the regulation of seasonal migration. Circadian or daily endogenous oscillators have been implicated in regulating day and night time activity in a