J Ornithol
DOI 10.1007/s10336-012-0817-3

REVIEW

Physiological and behavioral responses of migrants to environmental cues

Marilyn Ramenofsky · Jamie M. Cornelius ·
Barbara Helm

Received: 8 May 2011 / Revised: 10 November 2011 / Accepted: 16 January 2012

Abstract Migrant species express wide varieties of movement strategies that closely mirror patterns of resource distribution. Resources can vary predictably in space and time (e.g., seasonal peaks of productivity in temperate regions) or can be unpredictable in one or both dimensions. Evolution of migration strategies and the underlying physiological and behavioral mechanisms are therefore diverse, but similarities have been noted. To understand how migrants respond to environmental cues, we focus on species that represent extremes along a continuum between obligate versus facultative migratory behavior and address the physiological mechanisms regulating these movements. Obligate migrants, which travel on highly predictable schedules, generally rely on the annual change in daylength and circannual rhythms to initiate the vernal and, where known, the fall phases of migration. Facultative species may show similar seasonal preparations in cases where resources are temporally predictable, but appear to rely more heavily upon local supplementary cues in the environment to initiate migrations. In general, the physiological response mechanisms to environmental cues that coordinate migratory movements include perception of the environmental cue and transduction to neuroendocrine and endocrine systems. Clearly, there are huge gaps in our knowledge in this area, but published studies of each of the migratory types suggest striking parallels. Based on a comparison of the physiological aspects of the divergent migratory patterns, we emphasize that the migratory types are not completely distinct. Instead, the differences of migration patterns and responsiveness to cues reflect differences in the relative contributions of common physiological mechanisms that underly the control of movements. A more complete understanding of migratory physiology requires continued descriptive studies, particularly in a greater diversity of model systems, in addition to experimental methods that utilize innovative tracking technology as well as behavioral and physiological innovations to draw attention to different levels of organization. Comprehending the physiological mechanisms underlying migratory patterns will be vital for knowing how migrants respond to current environmental cues and anticipating their reactions to future conditions.

Keywords Environmental conditions · Predictable cues · Unpredictable cues · Obligate migrants · Facultative migrants · Hypothalamic-pituitary axis

Introduction

Migrants experience a broad spectrum of environmental conditions throughout their annual cycle, including changes in habitat, type, and availability of resources, predation, weather, social conditions, photoperiod, and levels of illumination (e.g., Newton 2008, 2011). To maintain

Communicated by Cristina Yumi Miyaki.

M. Ramenofsky (✉)
Neurobiology Physiology Behavior, University of California,
Davis, CA 95616, USA
e-mail: marramsky@gmail.com

J. M. Cornelius · B. Helm
Vogelwarte Radolfzell Max Planck Institute for Ornithology,
Schlossallee 1 a, 78315 Radolfzell, Germany
e-mail: cornelius@ucdavis.edu

B. Helm
Universität Konstanz, 78457 Konstanz, Germany
e-mail: helm@orn.mpg.de

homeostasis across such varieties of conditions, birds and other organisms undergo dynamic adjustments of physiological and behavioral states (i.e., phenotypic flexibility). Migrants are thereby better equipped to meet the demands of dynamic conditions than if a fixed phenotype is maintained (Piersma and Van Gils 2011). To time such adjustments correctly, migrants must filter relevant environmental stimuli from random fluctuations and maintain a balance between programmed and flexible schedules. Importantly, responses to environmental factors must be fitted to particular ecologies of migratory populations. Birds show a wide range of movement strategies that reflect diverse patterns of resource distributions. These resources can vary predictably or unpredictably in space and time and, therefore, migration strategies and the underlying physiological and behavioral mechanisms that control them are varied. Thus, migration comprises a spectrum of types, with precisely timed long-distance movements at one extreme, and facultative and nomadic at the other, and many intermediary forms inbetween, with large overlap of strategies sometimes even within populations (Chan 2005; Newton 2008, 2011). Here, we highlight different strategies focusing on two general types from the extremes of migratory patterns. These include obligate migrants, which carry out seasonal movements each year at similar times, and facultative species, which show great variability in timing and locations of their movements (Newton 2008, 2011). Comparing responses of different types of migrants to environmental conditions and their mechanistic basis is the central theme of this review as well as an attempt to reassess the distinctions across these apparent groupings.

Environmental factors influence migration

Cues in the environment guide organisms in synchronizing the onset, progression, and termination of life history stages throughout the annual cycle with conditions that typically can support them (Ramenofsky and Wingfield 2007; Wingfield 2008a, b; Visser et al. 2010; Newton 2011). Patterns of food abundance and weather are considered ultimate factors that select individuals which migrate and breed when conditions are most suitable (Baker 1938; Perrins 1970; Wingfield 2008a, b). If organisms coordinate their activities with these conditions, they can breed successfully and secure survival until the next reproductive opportunity. However, matching life-cycle stages to suitable conditions requires that phenotypic adjustments be made in anticipation of later events. Onset of such preparations may be initiated by environmental cues, often in combination with circannual (from Latin *circa* = about and *annus* = year) clocks (Farner 1955; Gwinner 1996; Helm et al. 2009). The use of environmental cues involves perception by the CNS followed by transduction to neuroendocrine and endocrine signals that regulate specific morphological, behavioral, and physiological systems. Cues can be divided into several general categories (Wingfield et al. 1990; Ramenofsky and Wingfield 2007). Initial predictive information includes permanent and reliable cues that possess both proximate (immediate) as well as predictive (long-term) values. The annual change in daylength or photoperiod supplies immediate and seasonal information to which the hypothalamic–pituitary–gonad axis (HPG) responds. While this axis is mainly responsible for seasonal activation of the reproductive system, the various life-cycle stages are linked to each other and, consequently, cues that act on the HPG are also relevant for the timing of migration. The cue can act directly as a driver or as a *Zeitgeber*, time giver, to entrain underlying circannual rhythms (Wingfield et al. 1990; Gwinner 1996; Ramenofsky 2011). Local supplementary cues provide information about the current conditions to either promote or slow the progress of migration. For example, some local supplementary cues upon which migrants rely include climatic conditions, social interactions, resource availability, habitat alterations, and predator density (Helm et al. 2006, Newton 2008, 2011; Both 2010; Végvári et al. 2011; Wingfield and Ramenofsky 2011). The availability and usefulness of these various cues depend on habitat type, resource use, and ecology of migrant species. There are also differences in the mechanisms by which information from these cues is processed by birds.

Predictability of cues and response mechanisms

The most predictable cue, at least during part of the annual cycle, is the change in daylength to which the HPG responds. Responses of migrants to this cue are highly specific, so that species and populations differing in migration phenology also show differences in cue responsiveness (Gwinner 1988; Helm et al. 2009). Furthermore, a migrant's response to cues is not static but varies over the annual cycle. The alternating states described as phenotypic flexibility involve changes in many physiological processes (Piersma and van Gils 2011), including perception, transduction, and response to cues (Wingfield 2008a, b; Visser et al. 2010). In the annual cycle, the vernal increase in daylength is perceived by the migrant and promotes development of several life-cycle stages: often prenuptial molt, then vernal migration and breeding, each with its attendant physiological and behavioral changes (Ramenofsky and Wingfield 2006). As the season progresses, daylengths commensurate with those that initiated the cycle are no longer perceived as stimulatory, a condition that has been termed photorefractoriness (Moore et al.

1982; Nicholls et al. 1988; Hahn et al. 2009). Breeding is terminated, indicating that exposure to environmental conditions (i.e., long days) that initiated the endocrine and behavioral responses in the vernal stage are no longer effective in the fall (Dawson et al. 2001). Ensuing fall events are related to the prior vernal stimulation of the HPG, but species differ in the interplay between long-term timing and effects of further environmental and behavioral factors (Hahn et al. 1997). In some species, physiological coupling between life-cycle stages appears to be so strong that fall processes follow suit despite variation in environmental conditions or individual experiences. This is suggested by experiments in the laboratory as well as by observations from free-living migrants that indicate extremely tight coupling between spring and fall migration (e.g., Conklin et al. 2010). Vernal activation acts as a “remote timer” for the termination of breeding, which for some species is followed by postnuptial molt then migratory fattening and fall migration (King and Farner 1963; Farner et al. 1980; Moore et al. 1982; Helm and Gwinner 2005). Other species show renewed photoperiodic sensitivity in the fall, a time when events are accelerated by shortening photoperiods (Hahn et al. 1997, 2009; Noskov et al. 1999; Dawson et al. 2000; Helm et al. 2009). These examples demonstrate that a given cue may be interpreted in specific and opposing ways depending on current stage of the life cycle (Visser et al. 2010). Furthermore, owing to this specificity, responses to cues can be fine-tuned by natural selection to achieve precise timing for a given species or population of migrants (Coppack and Pulido 2004; Helm et al. 2009).

In addition to initial predictive cues, local supplementary cues are more temporally and spatially variable, and can act to modulate the rate of progression through a life-history stage (Wingfield et al. 1990; Ramenofsky and Wingfield 2007). Such supplementary cues include temperature, rainfall, food resources, social conditions, etc. all of which fall within the prescribed range to which a species is able to respond within the given life-history stage (Wingfield et al. 1996, 2003). In both migratory types, supplementary cues can activate the HPG (Hahn et al. 1997; Hau et al. 2004; Voigt et al. 2007). In contrast, responses to unpredictable cues involve a second neuroendocrine pathway, the hypothalamic–pituitary–adrenal axis (HPA). The HPA is associated with the emergency life history stage, which is regarded as a process of redirecting behavior and physiology away from the immediate life-history stage to reduce the impact of immediate negative conditions (Wingfield and Ramenofsky 1999; Wingfield and Romero 2001). The neuroendocrine and endocrine mediators of the HPA include neuropeptides (CRF), pituitary proteins and peptides (ACTH, endorphins, enkephalins), and adrenal glucocorticoids to name a few (Claes 2004; Wingfield and Romero 2001). In particular, corticosterone, an adrenal glucocorticoid, is known to influence the acute behavioral and physiological responses to unpredictable conditions that migrants may employ. These include increased foraging behavior, fattening to fuel impending movement, metabolic adjustments to maintain homeostasis, and initiation of escape or irruptive movements (Wingfield 2003). As described below, both the HPG and HPA may contribute to the precise timing and type of migration.

Migration strategies and cues responses as a continuum

Obligate and facultative migrants have traditionally been distinguished by the ecology of their movements and, correspondingly, their presumed use of predictive and local cues for timing life-cycle stages (Newton 2008, 2011). For obligate migrants, food resources are predictable on a seasonal basis—temporally available during the breeding stage but quickly become scarce thereafter. Thus, migrants move to overwintering locations where resources are sufficiently plentiful to support life, but are distant from where breeding occurs. Accordingly, obligate migrants predominantly rely on initial predictive cues and circannual clocks to initiate the preparatory phases for movement to permanent breeding or overwintering sites. Some obligate migrant species are so punctual that they show almost complete consistency in timing between years (e.g., Battley 2006; hence called “calender birds”, Newton 2011). In many others, however, actual departure may be influenced by local supplementary cues, the nature of which is not well understood. For example, birds time departure from the breeding grounds when resources still abound, utilizing cues such as weather, social environment, physiological condition, etc. (Richardson 1990; Gauthreaux 1991; Morton 1992; Jenni and Kéry 2003; Jenni and Schaub 2003; Helm et al. 2006; Newton 2008). Furthermore, reduction in the availability of food has been shown to modify the migration programme during spring departure (Studds and Marra 2011) and en route in fall (Fusani et al. 2011). Such reliance on both initial predictive and local supplementary cues suggests that obligate migrants show facultative components within their annual movements (Newton 2011), a point raised earlier by Helms (1963) and Terrill (1990). For example, though initiation of fall and vernal migration may be obligate (Morton 2002; Newton 2008, 2011), subsequent phases often become more facultative as birds adjust to changing conditions during flight and stopovers. Such facultative aspects in at least some obligate migrant species make the timing, orientation of flight, and distance traveled variable (Helms 1963; Terrill and Ohmart 1984; Newton 2008, 2011). The physiological mechanisms regulating these movements are reminiscent of more facultative species.

One distinction that particularly defines facultative migrants is that they show a greater responsiveness to local supplementary cues. Their movements are a response to resources that are unpredictably available in space and/or time. Facultative migrants must, therefore, perceive and assess current conditions and respond by either remaining in an area or moving to a distant and more profitable location. The greater responsiveness to environmental conditions is particularly apparent in the fall when many irruptive species make decisions to migrate or remain resident at the breeding grounds. This temporal flexibility, in combination with generally shorter migration distances, allows for more precise matching of arrival time to local conditions in a given year (hence the term "weather birds"; Newton 2011). Orientation, distance, and timing of fall departure of facultative migrants can be much more variable than in obligate migrants (Newton 2011). Because of their less defined nature, facultative migrations are not as well understood as those of obligate species. Existing work suggests that migratory decisions depend on combination of a genetic window of "readiness" to move and sensitivity to environmental and social factors, which in turn may vary between individuals within populations (Adriaensen and Dhondt 1990; Chan 2005; Helm and Gwinner 2006; Palacín et al. 2011; Newton 2011). Among the best-explored taxa are species that reside on the extreme end of facultative migration, i.e., nomadic and irruptive Red Crossbills, *Loxia curvirostra* and *L. leucoptera* (Hahn 1998; Deviche and Sharp 2001). On an annual basis, Red Crossbills respond, as do obligate migrants, to the initial predictive increase in daylength that affects the developmental phases of migration and breeding (Berthold 1977; Hahn 1998; Deviche and Sharp 2001; Newton 2008). During breeding, Red Crossbills feed almost exclusively upon coniferous cone seeds, whose availability and abundance in any given year are unpredictable in space and, to some extent, time. In winter and spring, if the local cone crop remains abundant and if individuals are paired, birds will remain in an area and breed (Hahn et al. 2008). However, new seed crops begin to develop in the late spring and early summer in many conifer species. Thus, if the local cone crop proves insufficient and/or population density is high, individuals will move nomadically during the summer to a distant site of which the dates of arrival, orientation of flight, distance covered, and number of individuals involved are both variable and largely undescribed, particularly in North America (Hahn et al. 2008; Newton 2008; Cornelius 2009). However, nomadic movements can transition into irruptive movements if large numbers of Crossbills fail to locate newly developing cone crops in their typical habitat range, leading to their appearance in atypical habitats. Although data remain limited, similarly hybrid, dynamic migration systems may exist in Australian and African nomadic species (Dingle 2008).

Proposed physiological mechanisms

Obligate migrants

From a breeding-range perspective, a migration cycle is initiated in the fall when a bird prepares to leave the breeding area. However, from a physiological perspective, the fall functions are coupled with vernal events, the latter of which have been most rigorously studied in obligate migrants. In these cases, species rely on initial predictive cues to time arrival at the breeding areas. These may include a direct response of photoperiod on the wintering grounds and/or entrainment of circannual rhythms to a decreased or constant photoperiod, both of which precipitate the onset of the developmental phases of vernal migration and breeding (Fig. 1). The physiological mechanisms regulating this phase of migration are known in part for a number of obligate migrants including Dark-eyed Junco, *Junco hyemalis* (Rowan 1926), *Zonotrichia* sparrows (Weise 1967; Morton and Mewaldt 1962; Stetson and Erickson 1972; Schwabl and Farner 1989, Wingfield et al. 1990), Garden Warbler, *Sylvia borin* (Gwinner 1988; Bluhm et al. 1991), Bobolink, *Dolichonyx oryzivorus* (Hamner and Stocking 1970), Red-headed Bunting, *Emberiza bruniceps* (Thapliyal et al. 1983), Black-headed Bunting, *Emberiza melanocephala* (Tewary and Kumar 1981), and European Quail, *Coturnix coturnix* (Boswell et al. 1993). Generally, what is known is that in species wintering in the northern hemisphere, daylength either preceding or following winter solstice acts as the initial predictive cue. In contrast, for cross-equatorial migrants, days are long upon arrival on the winter grounds and start to shorten after the solstice. In these species, the photoperiodic response mechanism is modified, and activation is initiated under shortening or constant daylength (Hamner and Stocking 1970; Bluhm et al. 1991; Gwinner 1988). The initial predictive cue activates release of androgen, the source of which is thought to be either adrenal gland or possibly brain, as its secretion is associated without an increase in pituitary luteinizing hormone (LH) (Wingfield and Farner 1978; Boswell et al. 1995a) (Fig. 1a). Androgens at this time influence the brain by organizing orexigenic neurons in the ventral medial hypothalamus (Deviche 1992; Boswell 2005), in essence serving to increase sensitivity of these neurons to central prolactin (PRL), neuropeptide Y (NPY), peptide YY, and possibly thyroid hormones (Yokoyama 1976; Denbow

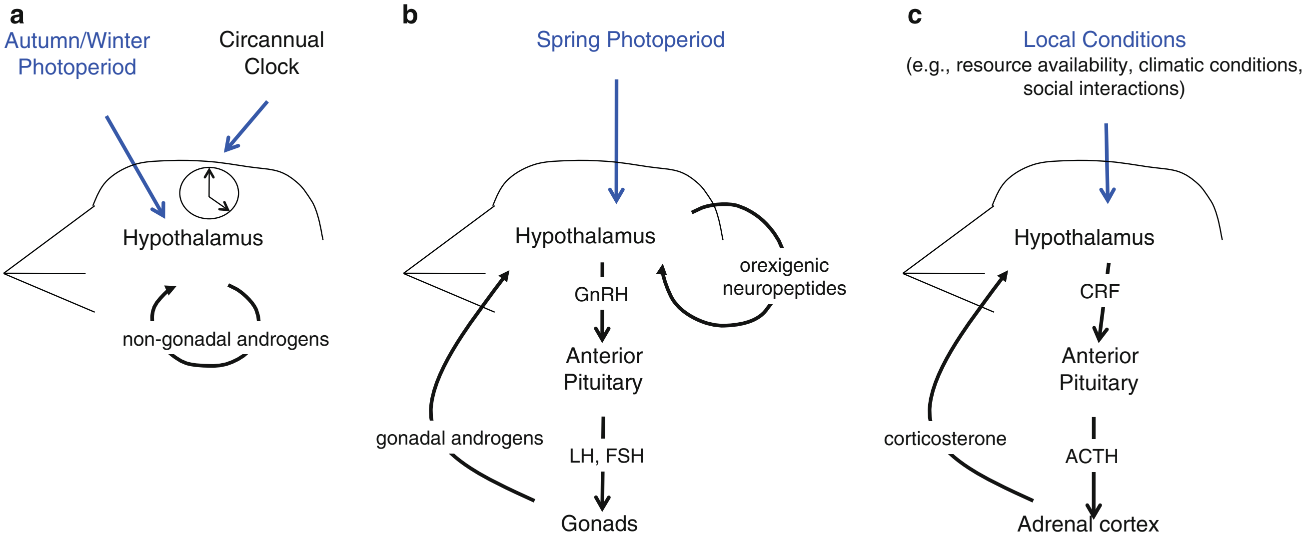

Fig. 1 Sequential steps for the proposed mechanisms underlying the developmental phase of vernal migration in obligate species. *Blue* lettering refers to environmental cues, *black* lettering represents the physiological and behavior responses. **a** Initial predictive factors (e.g., fall or winter photoperiod) and/or the circannual clock trigger the preparatory phases of migration. Secretion of androgen from either the adrenal cortex or the brain acts by organizing the hypothalamic neurons in feeding centers within the brain (Boswell et al. 1993). **b** Photoperiod reaches critical daylength in spring and enhances release of orexigenic neuropeptides that induce hyperphagia that is followed by fattening. Photoperiodic stimulation of the hypothalamic–pituitary–gonad axis (HPG) results in secretion of gonadal androgen. This may stimulate enhanced feeding, flight muscle hypertrophy, erythropoiesis, and attainment of migratory disposition. **c** Actual departure of birds in migratory disposition is influenced by local supplementary cues that include availability of food resources, weather, social interactions, etc. Note parallels to facultative movements (see Fig. 2) (color figure online)

et al. 1988; Kuenzel and McMurtry 1988), while reducing sensitivity to the anorexic effects of cholecystokinin (CCK) (Boswell et al. 1995a, b; Richardson et al. 1995). Once the increasing vernal photoperiod reaches the critical daylength for a particular species, the HPG axis is activated (Fig. 1b). At the central level, prolactin and neuropeptides bind to the sensitized hypothalamic receptors and affect hyperphagia and fattening. In the periphery, gonadal androgen enhances further fattening, increased body mass, and flight muscle hypertrophy (Wingfield et al. 1990; Tonra et al. 2011; Z. Neméth, unpublished data). Associated with the muscle hypertrophy is the deposition of lipid by enhanced fatty acid transport proteins in the membrane and increased heart type fatty acid binding protein within the sarcolemma (McFarlan et al. 2009). The enhanced lipid within the muscle provides necessary substrates for β oxidation of fatty acids and ATP production for sustained flight (Marsh 1984; Price et al. 2011). Some other developmental facets include erythropoiesis, resulting in increased hematocrit to enhance the oxygen-carrying capacity of the blood, and changes in diel patterns of activity in those species that become night active for nocturnal migratory flight (Piersma et al. 1996; Morton 2002; Ramenofsky et al. 2008). Once the developmental phase is complete, birds achieve migratory disposition and are ready to depart. Actual departure, progression to breeding grounds, and final termination of the spring migratory phase are influenced mainly by local supplementary factors that include weather, food availability, and specific conditions on the ground (Fig. 1c). The physiological mechanisms of these phases are poorly understood, but there is evidence that the relative importance of different cues varies between species and over the course of the migration season (Duriez et al. 2009).

For most species, the physiological preparation for fall migration resembles that of the vernal phase. As suggested above, in obligate migrants, fall events appear to be closely coupled to vernal processes, although the physiological basis of the coupling is not well understood. Studies suggest that the degree of coupling and the importance of timers differ between species. According to laboratory studies, some migratory species resume fall processes after termination of reproduction regardless of photoperiodic manipulations, indicating that endogenous circannual clocks suffice to drive the transition between life-cycle stages (Gwinner 1988, 1996; Helm 2006; Piersma et al. 2008). In these and other species, photoperiodic exposure during spring can influence the scheduling of subsequent breeding, molt, and fall migratory events (King and Farner 1963; Farner et al. 1980; Moore et al. 1982). For example, Stonechats (*Saxicola torquata*) respond to subtle differences in daylength during spring migration and thereby set schedules for the events leading up to the initiation of fall migratory restlessness (Helm and Gwinner 2005; Helm et al. 2009). In a display of further flexibility, some species remain sensitive to photoperiodic cues later in the breeding season to adjust the timing and speed of fall processes. For example, many species accelerate or interrupt molt and advance migratory preparations when photoperiod and other predictors indicate imminent deterioration of environmental conditions (e.g., Jenni and Winkler 1994; Hahn et al. 1997; Noskov et al. 1999; Kullberg et al. 2003).

Annual schedules can be further influenced by modification of life-cycle events, e.g., by late breeding, which in turn has been shown to delay fall processes in migratory birds via endocrine mechanisms (e.g., Wingfield and Farner 1979). However, the degree to which such modifications occur appears to be associated with migratory programming. In various species of long-distance migrants, spring and fall migration dates are closely linked, indicating little flexibility in timing. For example, in Bar-tailed Godwits (*Limosa lapponica baueri*) order of departure in vernal and fall migrations correlate with a coefficient of 0.74 (Conklin et al. 2010). Based on such observations, the argument has been made that long-distance migrants are more physiologically constrained in their ability to take advantage of a lengthening breeding season, while shorter-distance migrants show greater sensitivity to environmental cues and are able to increase the number of annual clutches, thus delaying onset of postnuptial molt and migration (Jenni and Kéry 2003; Jenni and Schaub 2003).

Facultative migrants

By comparison, the physiological mechanisms that regulate movements of facultative migrants are less well described than those of obligate migrants. Facultative movements that are seasonally predictable may nonetheless include similar preparatory mechanisms as those of obligate migrants (Fig. 2). For example, free-living Red Crossbills show a seasonal vernal peak in fat that exceeds winter fattening and coincides with the seasonal development of new cone crops, suggesting that the predictive cues might be utilized to prepare for spring facultative movements (J. Cornelius, unpublished data). In support of this hypothesis, captive Red Crossbills held on the constant photoperiod of a 12L:12D (light:dark cycle) express a circannual endogenous rhythm of fattening which peaks in the spring (Berthold 1977). It remains unknown if other physiological preparations occur seasonally or if local conditions must stimulate further migratory preparations, as is almost certain to be the case for the decisions regarding migratory departure. African Red-billed Queleas (*Quelea quelea*) have robust annual cycles in captivity but can be nomadic and even itinerant breeders in the wild. Queleas deposit migratory fat reserves after breeding, but whether or not they initiate migration may depend on factors that vary unpredictably (Dallimer and Jones 2002). Australian Silvereyes, *Zosterops lateralis*, display a range of behaviors extending from resident to facultative even nomadic migratory movements. Each strategy is inherited with specific thresholds to social stimuli and demonstrating differential degrees of migratory fattening (Chan 2005). Thus, a variety of species that display facultative to irruptive migratory patterns nonetheless show underlying seasonal changes in fattening similar to obligate migrants.

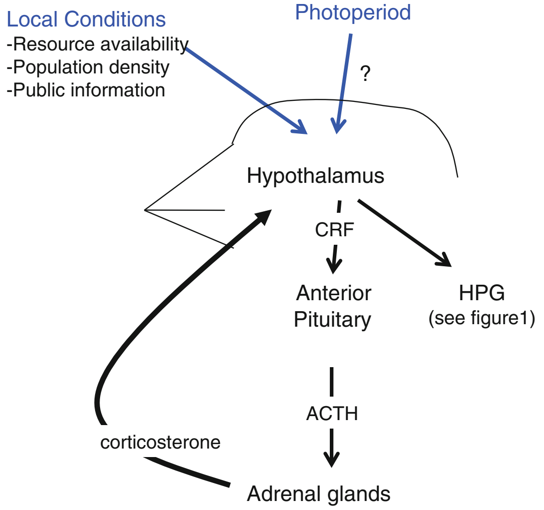

Fig. 2 Proposed mechanisms for regulation of both stages of migratory activity of a facultative migrant. *Blue* lettering refers to environmental cues and *black* lettering represents the physiological and behavioral responses. Preparatory mechanisms may be similar to those described for the obligate migrant if resources are predictable. Actual departure decisions, however, may rely more heavily upon the hypothalamic–pituitary–adrenal axis (HPA) and release of corticosterone with its central effects on behavior and physiology. Reduction in available food or observations of feeding activity of flock mates activates the HPA causing an increase in production and secretion of plasma corticosterone, which in turn affects the departure from a local site. Note that both migratory categories share physiological mechanisms, the distinctions of which are dependent upon the life-cycle context of the movement and predictability of resources in time and space (color figure online)

Although movements may occur throughout the year, in most species they are concentrated in either the vernal or fall phase. Breeding can immediately follow facultative movements if the movement brings individuals into adequate resources (Hahn et al. 1997; Perfito et al. 2007; Hahn and MacDougall-Shackleton 2008). The HPG axis must, in those cases, be responsive and the gonads in near ready condition for breeding, particularly if breeding opportunities are otherwise limited. In any case, the mechanisms underlying facultative movements are probably quite diverse, depending upon both the life-cycle context of the movement and on the spatial or temporal predictability of the contingent resources surrounding the movement.

Facultative movements that occur in response to sudden or unpredictable fluctuations in environmental conditions are thought to be linked to the stress response systems. Adrenal glucocorticoids and, specifically, corticosterone in birds play a regulatory role in metabolism, energy balance, behavior, and the emergency life-history stage (Wingfield 2008a, b; Romero et al. 2009). Many studies have identified a relationship between elevated plasma levels of corticosterone and variable conditions of weather, social interactions, food availability, and predators (Terrill 1987; Astheimer et al. 1992; Silverin 1997; Landys-Ciannelli et al. 2002; Hahn et al. 2004). Food restriction, unpredictable food delivery, or prolonged dim light conditions that resulted in sustained migratory restlessness were associated with increased levels of baseline corticosterone in captive birds (Pravosudov et al. 2001; Reneerkens et al. 2002b; Lynn et al. 2003; Ramenofsky et al. 2008). A number of studies of obligate migrants have similarly identified elevated levels of baseline corticosterone at departure as well as during long-distance flight, circumstances where birds face conditions of uncertainty and high energy demand (Falsone et al. 2009; Landys-Ciannelli et al. 2002; Piersma et al. 2000; Reneerkens et al. 2002a; Lohmus et al. 2003). Taken together, these findings suggest that conditions that are unpredictable and/or convey a measurable degree of uncertainty induce a neuroendocrine response resulting in elevated corticosterone. The resulting elevated levels may help to redirect behavioral and physiological processes to reduce the impending negative impact of the unpredictable event (Fig. 2). Often, this includes changes in movement behavior, including potential induction of emergency or escape migrations (Wingfield 2003). For example, experimentally elevated corticosterone increases the activity range of free-living Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) as much as 800%, and increases the probability that individuals will make facultative altitudinal migrations to lower elevations during spring storms (Breuner and Hahn 2003). Irruptive migratory behavior may similarly be influenced by corticosterone during low or declining food conditions, though experimental field studies remain lacking (Cornelius et al. 2010).

In some species of migrant, social aggregation can be important determinants of departure under given environmental conditions (Helm et al. 2006; Newton 2008). Social cues can further influence coordination, direction, and timing of movements. New studies are beginning to shed light on the ways that information spreads from one individual to another within the flock. For example, behavioral studies suggest that Red Crossbills make decisions informed by observations of other foraging individuals. Information spread across members of the flock, called public information, influenced departure rates from the current foraging location (Smith et al. 1999). Such a process can effectively improve the assessment of an unpredictable resource and coordinate pair or flock movements. A similar phenomenon may occur in captive Australian Silvereyes where migratory behavior in one individual can stimulate the development of migratory behavior in neighboring individuals (Chan 2005). One physiological mechanism has recently been tested. Food restriction in captive Red Crossbills resulted in decreased deposits of fat, elevation of baseline corticosterone, and increased locomotor activity. However, public information may have influenced the degree of behavioral and physiological response: birds with food-restricted neighbors showed higher corticosterone levels and a trend for higher activity during food restriction than those with neighbors who had food ad libitum (controls) (Cornelius et al. 2010). This suggests that public information may be used as a proxy or estimate of the productivity of a local site and that corticosterone may serve as an endocrine mediator aiding in synchronizing movements between individuals (Fig. 2).

Conclusions

Two migratory forms—obligate and facultative—are recognized as residing at each end of a spectrum (see Newton 2011). Separation of these types is largely explained by degree of obligation to move, arising from timing and predictability of the ultimate selective factor, namely the availability of food. In general, obligate species tend to move on regular bases of timing, direction, and distance flown, whereas facultative migrants vary in some or all of these regards. However, these patterns are not mutually exclusive, so that a given migrant can sequentially show different types of movement. Accordingly, there appears to be overlap in the physiological mechanisms employed. For obligate migrants, the endocrine mechanisms that regulate the developmental phases of migration largely consist of androgenic effects on the brain and pituitary, in relation to photoperiod and endogenous oscillators. Actual departure and subsequent movement decisions are then influenced more heavily by local conditions, which may be coordinated through the brain, pituitary, and adrenal axis reminiscent of the mechanisms observed in more facultative species. Migrants that move facultatively must undergo preparations for seasonal movements at particular times that are driven by the HPG and therefore reminiscent of obligatory migrants. Irruptive movements of facultative migrants, induced by declining local resources, probably involve activation of the HPA, which in turn may coordinate departure. Mechanisms controlling decisions of orientation, distance, and timing of these movements remain obscure.

Although our physiological understanding of these systems remains remarkably incomplete, it is becoming apparent that the distinctions between these migratory strategies may be less clear-cut then previously assumed (Newton 2011). Many species employ combinations of movement types and are responsive to many of the same environmental cues, but with differing degrees of sensitivity and/or timing of cue use. Furthermore, given our current understanding of the underlying control mechanisms, we suggest that the regulation of movements involves similar pathways in different types of migrants (i.e., the HPG and HPA), which differ in the relative impact of their contribution. We suspect that further description of the physiological mechanisms regulating how organisms respond to environmental cues in relation to migration will help to more accurately relate these migratory types to ecology, and lend insight into their evolutionary relationships. It is our hope that this contribution provides a stimulus for future studies. Deeper insights into the regulatory mechanisms of migration are critically important, as it remains unclear whether the behavior and physiology of migrants can keep pace with the rapidly changing phenologies of the planet (Wingfield 2008a, b; Knudsen et al. 2011; Visser et al. 2010).

Acknowledgments We wish to thank the organizers of the 25th International Ornithological Congress held in Campos do Jordão, Brazil, as well as the individual contributors to Symposium #26, *Migrant responses to environmental conditions: Integrating ecological and physiological approaches*: Professors Ian Newton and Barry Pinshow, Dr. Andrey Mukhin, and Mr. Peter S. Jorgensen. We also wish to thank Dr. Scott MacDougall-Shackleton and two anonymous reviewers for their helpful comments on the earlier drafts. Their contributions greatly improved the messages of our work. B.H. is supported by the European Social Fund in Baden-Württemberg. Many of the ideas presented herein were supported by a research grant from the National Science Foundation (IOS-0920791) to M.R.

References

Adriaensen F, Dhondt AA (1990) Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. J Anim Ecol 59:1077–1090

Astheimer LB, Buttemer WA, Wingfield JC (1992) Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Orn Scand 23:355–365

Baker JR (1938) The evolution of breeding season. In: DeBeer GB (ed) Evolution: essays on aspects of evolutionary biology. Oxford University Press, Oxford, pp 161–177

Battley PF (2006) Consistent annual schedules in a migratory shorebird. Biol Lett 2(4):517–520. doi:10.1098/rsbl.2006.0535

Berthold P (1977) Über eine mögliche endogene Steuerung der Zugdisposition beim Fichtenkreuzschnabel, *Loxia curvirostra*. J Ornithol 118:203–204

Bluhm CK, Schwabl H, Schwabl I, Perera A, Follett BK, Goldsmith AR, Gwinner E (1991) Variation in hypothalamic gonadotrophin-releasing hormone content plasma and pituitary LH, and in vitro testosterone release in a long-distance migratory bird, the garden warbler (*Sylvia borin*), under constant photoperiods. J Endocrinol 128:339–345

Boswell T (2005) Regulation of energy balance in birds by the neuroendocrine hypothalamus. J Poult Sci 42:161–181

Boswell T, Hall MR, Goldsmith AR (1993) Annual cycles of migratory fattening, reproduction and moult in European quail (*Coturnix coturnix*). J Zool Lond 231:627–644

Boswell T, Hall MR, Goldsmith AR (1995a) Testosterone is secreted extragonadally by European quail maintained on short days. Physiol Zool 68:967–984

Boswell T, Richardson RD, Seeley RJ, Ramenofsky M, Wingfield JC, Friedman MI, Woods SC (1995b) Regulation of food intake by metabolic fuels in white-crowned sparrows. Am J Physiol 269:R1462–R1468

Both C (2010) Flexibility of timing of avian migration to climate change masked by environmental constraints en route. Curr Biol 20:243–248

Breuner CW, Hahn TP (2003) Integrating stress physiology, environmental change, and behaviour in free-living sparrows. Horm Behav 43:115–123. doi:10.1016/s0018-506x(02)00020-x

Chan K (2005) Partial migration in the silvereye (*Zosteropidae*: Aves): pattern, synthesis, and theories. Ethol Ecol Evol 17:349–363

Claes SJ (2004) Corticotropin-releasing hormones (CRH) in psychiatry: from stress to psychopathology. Ann Med 36:50–61

Conklin JR, Battley PF, Potter MA, Fox JW (2010) Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. Nat Commun 1(6):67. doi:10.1038/ncomms1072

Coppack T, Pulido F (2004) Photoperiodic response and the adaptability of avian life cycles to environmental change. Adv Ecol Res 35:131–150. doi:10.1016/S0065-2504(04)35007-5

Cornelius J (2009) Annual schedules, environmental cues and stress physiology in an irruptive, nomadic songbird, the red crossbill (*Loxia curvirostra*). PhD thesis, University of California, Davis

Cornelius JM, Breuner CW, Hahn TP (2010) Under a neighbour's influence: public information affects stress hormones and behaviour of a songbird. Proc R Soc Lond B 277:2399–2404

Dallimer MJ, Jones P (2002) Migration orientation behaviour of the red-billed quelea *Quelea quelea*. J Avian Biol 33:89–94

Dawson A, Hinsley S, Ferns P, Bonser R, Eccleston L (2000) Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proc R Soc Lond B 267:2093–2098

Dawson A, King VM, Bentley GE, Ball GR (2001) Photoperiodic control of seasonality in birds. J Biol Rhythm 16:365–380

Denbow DM, Duke GE, Chaplin SB (1988) Food intake, gastric secretion, and motility as affected by avian pancreatic polypeptide administered centrally in chickens. Peptides 9:449–454

Deviche P (1992) Testosterone and opioids interact to regulate feeding in a male migratory songbird. Horm Behav 26:394–405

Deviche P, Sharp PJ (2001) Reproductive endocrinology of a free-living, opportunistically breeding passerine (white-winged crossbill, *Loxia leucoptera*). Gen Comp Endocrinol 123:268–279

Dingle H (2008) Bird migration in the southern hemisphere: a review comparing continents. Emu 108:341–359

Duriez O, Bauer S, Destin A, Madsen J, Nolet BA, Stillman RA, Klaassen M (2009) What decision rules might pink-footed geese use to depart on migration? An individual-based model. Behav Ecol 20:560–569

Falsone K, Jenni-Eiermann S, Jenni L (2009) Corticosterone in migrating songbirds during endurance flight. Horm Behav 56:548–556

Farner DS (1955) The annual stimulus for migration: experimental and physiologic aspects. In: Wolfson A (ed) Recent studies in avian biology. University of Illinois, Urbana, pp 198–237

Farner DS, Donham RS, Moore MC, Lewis RA (1980) The temporal relationship between the cycle of testicular development and molt in the White-crowned sparrow, *Zonotrichia leucophrys gambelii*. Auk 97:63–75

Fusani L, Cardinale M, Schwabl I, Goymann W (2011) Food availability but not melatonin affects nocturnal restlessness in a wild migrating passerine. Horm Behav 59:187–192

Gauthreaux SA Jr (1991) The flight behaviour of migrating birds in changing wind fields: radar and visual analyses. Am Zool 31:187–204

Gwinner E (1988) Photorefractoriness in equatorial migrants. Proc Int Ornithol Congr 19:626–633

Gwinner E (1996) Circadian and circannual programs in avian migration. J Exp Biol 199:39–48

Hahn TP (1998) Reproductive seasonality in an opportunistic breeder, the red Crossbill, *Loxia curvirostra*. Ecology 79:2365–2375

Hahn TP, MacDougall-Shackleton SA (2008) Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response system of birds. Philos Trans R Soc Lond B 363:267–286

Hahn TP, Boswell T, Wingfield JC, Ball GF (1997) Temporal flexibility in avian reproduction. Patterns and mechanisms. In: Nolan V, Ketterson ED, Thompson CF (eds) Current ornithology. Plenum, New York, pp 39–80

Hahn TP, Sockman KW, Breuner CW, Morton ML (2004) Facultative altitudinal movements by mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. Auk 121:1269–1281

Hahn TP, Cornelius JM, Sewall KB, Kelsey TR, Hau M, Perfito N (2008) Environmental regulation of annual schedules in opportunistically-breeding songbirds: adaptive specialization or variations on a theme of white-crowned sprarow? Gen Comp Endocrinol 157:217–226

Hahn TP, Watts HE, Cornelius JM, Brazeal KR, MacDougall-Shackleton SA (2009) Evolution of environmental cue response mechanisms: adaptive variation in photorefractoriness. Gen Comp Endocrinol 163:193–200. doi:S0016-6480(09)00163-4[pii]

Hamner WM, Stocking J (1970) Why don't bobolinks breed in Brazil? Ecology 51:743–751

Hau M, Wikelski M, Gwinner H, Gwinner E (2004) Timing of reproduction in a Darwins' finch: temporal opportunism under spatial constraints. Oikos 106:489–500

Helm B (2006) Zugunruhe of migratory and non-migratory birds in a circannual context. J Avian Biol 37:533–540

Helm B, Gwinner E (2005) Carry-over effects of day length during spring migration. J Ornithol 146:348–354. doi:10.1007/s10336-005-0009-5

Helm B, Gwinner E (2006) Migratory restlessness in an equatorial nonmigratory bird. PLoS Biol 4:611–614

Helm B, Piersma T, Van der Jeugd H (2006) Sociable schedules: interplay between avian seasonal and social behaviour. Anim Behav 72:1215

Helm B, Schwabl I, Gwinner E (2009) Circannual basis of geographically distinct bird schedules. J Exp Biol 212:1259–1269

Helms CW (1963) The annual cycle and Zugunruhe in birds. Proc Int Ornithol Congr 13:925–939

Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proc R Soc Lond B 270:1467–1471

Jenni L, Schaub M (2003) Behavioural and physiological reaction to environmental variation in bird migration: a review. In: Berthold PEGES (ed) Bird migration. Springer, Berlin, pp 155–171

Jenni L, Winkler R (1994) Moult and ageing of European passerines. Academic, London

King JR, Farner DS (1963) The relationship of fat deposition to Zugunruhe and migration. Condor 65:200–223

Knudsen E, Lindén A, Both C, Jonzén N, Pulido F, Saino N, Sutherland WJ, Bach LA, Coppack T, Ergon T, Gienapp P, Gill JA, Gordo O, Hedenström A, Lehikoinen E, Marra PP, Møller AP, Nilsson ALK, Péron G, Ranta E, Rubolini D, Sparks TH, Spina F, Studds CE, Sæther SA, Tryjanowski P, Stenseth NC (2011) Challenging claims in the study of migratory birds and climate change. Biol Rev 86:928–946. doi:10.1111/j.1469-185X.2011.00179.x

Kuenzel WJ, McMurtry J (1988) Neuropeptide Y: brain localization and central effects on plasma insulin levels in chicks. Physiol Behav 44:669–678

Kullberg C, Lind J, Fransson T, Jakobsson S, Vallin A (2003) Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). Proc R Soc Lond B 270:373–378

Landys-Ciannelli MM, Landys-Ciannelli MM, Ramenofsky M, Piersma T, Jukema J, Wingfield JC, Castricum Ringing Group (2002) Baseline and stress-induced plasma corticosterone during long-distance migration in the bar-tailed godwit, *Limosa lapponica*. Physiol Biochem Zool 75:101–110

Lohmus M, Sandberg R, Holberton RL, Moore FR (2003) Corticosterone levels in relation to migratory readiness in red-eyed vireos (*Vireo olivaceus*). Behav Ecol Sociobiol 54:233–239

Lynn SE, Breuner CW, Wingfield JC (2003) Short-term fasting affects locomotor activity, corticosterone, and corticosterone binding globulin in a migratory songbird. Horm Behav 43:150–157

Marsh RL (1984) Adaptations of the gray catbird *Dumetella carolinensis* to long-distance migration: flight muscle hypertrophy associated with elevated body mass. Physiol Zool 57:105–117

McFarlan JT, Bonen A, Guglielmo CG (2009) Seasonal upregulation of fatty acid transporters in flight muscles of migratory white-throated sparrows (*Zonotrichia albicollis*). J Exp Biol 212:2934–2940

Moore MC, Donham R, Farner DS (1982) Physiological preparation for autumnal migration in white-crowned sparrows. Condor 84:410–419

Morton ML (1992) Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrows. Condor 94:117–133

Morton ML (2002) The mountain white-crowned sparrow: migration and reproduction at high altitude. Stud Avian Biol 24:236

Morton ML, Mewaldt LR (1962) Some effects of castration on a migratory sparrow (*Zonotrichia atricapilla*). Physiol Zool 35:237–247

Newton I (2008) The migration ecology of birds. Academic, Oxford

Newton I (2011) Obligate and facultative migration in birds: ecological aspects. J Ornithol. doi:10.1007/s10336-011-0765-3

Nicholls TJ, Goldsmith AR, Dawson A (1988) Photorefractoriness in birds and comparison with mammals. Physiol Rev 68:133–176

Noskov G, Rymkevich T, Iovchenko N (1999) Intraspecific variation of molt: adaptive significance and ways of realisation. Proceedings of the 22nd international ornithological congress, vol 22. BirdLife South Africa, Johannesburg, pp 544–563

Palacín C, Alonso JC, Alonso JA, Magaña M, Martín CA (2011) Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard *Otis tarda*. J Avian Biol 42:301–308. doi:10.1111/j.1600-048X.2011.05395.x

Perfito N, Zann RA, Bentley GE, Hau M (2007) Opportunism at work: hatibtat predictability affects reproductive readiness in free-living zebra finches. Funct Ecol 21:291–301

Perrins CM (1970) The timing of birds' breeding seasons. Ibis 112:242–255

Piersma T, van Gils JA (2011) The flexible phenotype: a body-centred integration of ecology, physiology and behaviour. Oxford University Press, Oxford

Piersma T, Everaarts JM, Jukema J (1996) Build-up of red blood cells in refuelling bar-tailed godwits in relation to individual migratory quality. Condor 98:363–370

Piersma T, Reneerkens J, Ramenofsky M (2000) Baseline corticosterone peaks in shorebirds with maximal energy stores for migration: a general preparatory mechanism for rapid behavioural and metabolic transitions? Gen Comp Endocrinol 120:118–126

Piersma T, Brugge M, Spaans B, Battley PF (2008) Endogenous circannual rhythmicity in body mass, molt, and plumage of great knots (*Calidris tenuirostris*). Auk 125:140–148. doi:10.1525/auk.2008.125.1.140

Pravosudov VV, Kitaysky AS, Wingfield JC, Clayton NS (2001) Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*). Gen Comp Endocrinol 123:324–331

Price E, Staples JF, Milligan CL, Guglielmo CG (2011) Carnitine palmitoyl transferase activity and whole muscle oxidation rates vary with fatty acid substrate in avian flight muscles. J Comp Physiol B 181:565–573

Ramenofsky M (2011) Hormones in migration and reproductive cycles of birds. In: Norris D, Lopez KH (eds) Hormones and reproduction in vertebrates. Academic, San Diego, pp 205–236

Ramenofsky M, Wingfield JC (2006) Behavioural and physiological conflicts in migrants: the transition between migration and breeding. J Ornithol 147:135–145

Ramenofsky M, Wingfield JC (2007) Regulation of migration. Bioscience 57:135–143

Ramenofsky M, Moffat J, Bentley GE (2008) Corticosterone and migratory behaviour of captive white-crowned sparrows. International proceedings of ICA-CPB, pressures of life: molecules to migration, pp. 575–582

Reneerkens J, Morrison RI, Ramenofsky M, Piersma T, Wingfield JC (2002a) Baseline and stress-induced levels of corticosterone after a long migratory flight, preparation for breeding and during incubation of a high arctic breeding shorebird (red knot, *Calidris canutus*). Physiol Biochem Zool 75:200–208

Reneerkens J, Ramenofsky M, Piersma T (2002b) An experimental test of the relationship between temporal variability of feeding opportunities and baseline levels of corticosterone in a shorebird. J Exp Zool 293:81–88

Richardson WJ (1990) Timing of bird migration in relation to weather. In: Gwinner E (ed) Bird migration, physiology and ecophysiology. Springer, Berlin, pp 78–101

Richardson RD, Boswell T, Raffety BD, Seeley RJ, Wingfield JC, Woods SC (1995) NPY increases food intake in white-crowned sparrows: effect in short and long photoperiods. Am J Physiol Regul Integr Comp Physiol 268:1418–1422

Romero LM, Dickens MJ, Cyr NE (2009) The reactive scope model—a new model integrating homeostais, allostasis and stress. Gen Comp Endocrinol 55:375–389

Rowan W (1926) On photoperiodism, reproductive periodicity and the annual migrations of birds and certain fishes. Proc Boston Soc Nat Hist 38:147–189

Schwabl H, Farner DS (1989) Dependency on testosterone of photoperiodically-induced vernal fat deposition in female white-crowned sparrows. Condor 91:108–112

Silverin B (1997) The stress response and autumn dispersal behaviour in willow tits. Anim Behav 53:451–459

Smith JW, Benkman CW, Coffey K (1999) The use and misuse of public information by foraging red crossbills. Behav Ecol 10:54–62

Stetson M, Erickson JE (1972) Hormonal control of photoperiodically induced fat deposition in white-crowned sparrows. Gen Comp Endocrinol 19:355–362. doi:10.1016/0016-6480(72)90118-9

Studds CE, Marra PP (2011) Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proc R Soc Lond B 278:3437–3443. doi:10.1098/rspb.2011.0332

Terrill SB (1987) Social dominance and migratory restlessness in the dark-eyed junco (*Junco hyemalis*). Behav Ecol Sociobiol 21:1–11

Terrill SB (1990) Ecophysiological aspects of movements by migrants in the wintering quarters. In: Gwinner E (ed) Bird migration. Physiology and ecophysiology. Springer, Berlin, pp 130–143

Terrill SB, Ohmart RD (1984) Facultative extension of fall migration by yellow-rumped warblers (*Dendroica coronata*). Auk 101:427–438

Tewary PD, Kumar V (1981) Effects of castration on photoperiodically induced weight gain, in a migratory finch: black-headed bunting (*Emberiza melanocephala*) (Aves). Indian J Exp Biol 19:469–471

Thapliyal JP, Lal P, Pati AK, Gupta BBP (1983) Thyroid and gonad in the oxidative metabolism, erythyropoiesis, and light response of migratory red-headed bunting, *Emberiza bruniceps*. Gen Comp Endocrinol 51:444–453

Tonra CM, Marra PP, Holberton RL (2011) Early elevation of testosterone advances migratory preparation in a songbird. J Expertl Biol 214:2761–2767

Végvári Z, Barta Z, Mustakallio P, Székely T (2011) Consistent avoidance of human disturbance over large geographical distances by a migratory bird. Biol Lett 7:814–817. doi:10.1098/rsbl.2011.0295 (online early)

Visser ME, Caro SP, van Oers K, Schaper SV, Helm B (2010) Phenology, seasonal timing and circannual rhythms: towards a unified framework. Philos Trans R Soc Lond B 365:3113–3127

Voigt C, Goymann W, Leitner S (2007) Green matters! Growing vegetation stimulates breeding under short-day conditions in wild canaries (*Serinus canaria*). J Biol Rhythm 22:554–557

Weise CM (1967) Castration and spring migration in the white-throated sparrow. Condor 69:49–68. doi:10.2307/1366372

Wingfield JC (2003) Avian migration: regulation of facultative-type movements. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin, pp 113–126

Wingfield JC (2008a) Organization of vertebrate annual cycles; implications for control mechanisms. Philos Trans R Soc Lond B 363:425–441

Wingfield JC (2008b) Comparative endocrinology, environment and global change. Gen Comp Endocrinol 157:207–216

Wingfield JC, Farner DS (1978) The annual cycle of plasma irLH and steroid hormones in feral populations of the white-crowned sparrow, *Zzonotrichia leucophrys gambelii*. Biol Reprod 19:1046–1056

Wingfield JC, Farner DS (1979) Some endocrine correlates of renesting after loss of clutch or brood in the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. Gen Comp Endocrinol 38:322–331. doi:10.1016/0016-6480(79)90066-2

Wingfield JC, Ramenofsky M (1999) Hormones and behavioural ecology of stress. In: Balm PHE (ed) Stress phyisology of animals. Sheffield University Press, Sheffield, pp 1–51

Wingfield JC, Ramenofsky M (2011) Hormone-behavior interrelationships of birds in response to weather. In: Brockmann HJ, Roper TJ, Naguib M, Mitani JC, Simmons LW (eds) Advances in the study of behavior, vol 43. Academic, Burlington, pp 93–188

Wingfield JC, Romero LM (2001). Adrenocortical responses to stress and their modulation in free-living vertebrates. In: McEwen BS (ed) Handbook of physiology, section 7, the endocrine system, vol 4: coping with the environment: neural and endocrine mechanisms. Oxford University Press, Oxford, p. 211 e236

Wingfield JC, Schwabl H, Mattocks PW Jr (1990) Endocrine mechanisms of migration. In: Gwinner E (ed) Bird migration: physiology and ecophysiology. Springer, Berlin, pp 232–256

Wingfield JC, Hahn TP, Wada M, Ashteimer LB, Schoech S (1996) Interrelationship of day lenth and temperature on the control of gonadal development, body mass, and fat score in white-crowned sparrows, *Zonotrichia leucophrys gambelii*. Gen Comp Endocrinol 101:242–255

Wingfield JC, Hahn TP, Maney DL, Schoech SJ, Wada M, Morton ML (2003) Effects of temperature on photoperiodically induced reproductive development, circulating plasma luteinizing hormone and thyroid hormones, body mass, fat deposition and molt in mountain white-crowned sparrows, *Zonotrichia leucophrys oriantha*. Gen Comp Endocrinol 131:143–158

Yokoyama K (1976) Hypothalamic and hormonal control of photoperiodically induced vernal functions in the white-crowned sparrow *Zonotrichia leucophrys gambelii*. I. The effects of hypothalamic lesions and exogenous hormones. Cell Tissue Res 174:391–416