

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.

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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.

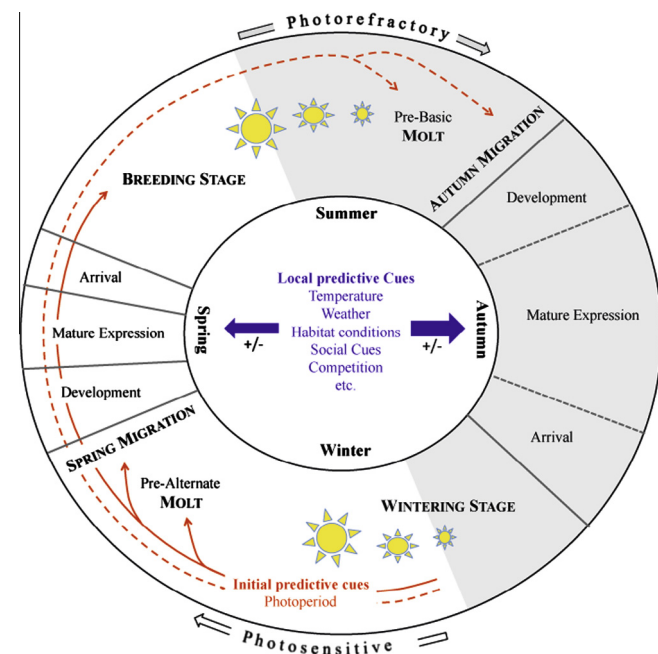


Fig. 1. Theoretical model of the effects of environmental conditions on spring and autumn stages of migration based on studies of north temperate overland migrants. Progression of the annual schedule is read in the clockwise direction. Initial predictive cues, in synergy with underlying endogenous rhythms, 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 postnatal 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.

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).

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

number of seasonally migrant species (Bartell and Gwinner, 2005; Coppack et al., 2008; Gwinner, 1996; McMillan et al., 1970; Rani et al., 2006). In these species, day length is considered to act as a *Zeitgeber* (or time giver) for the endogenous circannual rhythm (Gwinner, 1986, 1996), but is not required for expression of cyclical patterns of behavior and physiology. The north temperate migrant dark-eyed junco (*Junco hyemalis*), for example, exhibited recurring cycles of gonadal growth, molt and *Zugunruhe* when held on constant dim light (1–3 Lux) for 3 years (Holberton and Able, 1992). The tropical spotted munia (*Lonchura punctulata*) produced similar testicular cycles when exposed to either constant LL, DD or 12L:12D conditions (Chandola et al., 1983). Without an external cue, however, cycles across the subjects in both studies drifted out of phase with one another. Similar endogenous rhythms in migratory physiology or behavior have been found in many seasonal migrants (reviewed in Gwinner and Helm (2003)). Even the nomadic migrant red crossbill (*Loxia curvirostra*), which makes an annual migration in the late spring to locate new conifer seed crops, exhibited recurring annual cycles of fattening when held for multiple years on 12L:12D (Berthold, 1977), similar to the annual cycle of fattening observed in wild conspecifics (Cornelius and Hahn, 2012). Together these data identify the existence of endogenous rhythms in a wide variety of migrant and non-migrant species that are expressed in the absence of fluctuations in the exogenous photoperiodic cue. Thus, the initial predictive factor regulating the onset of the spring and autumn stages in many migrants involves a photoperiodic cue that entrains or synchronizes an underlying endogenous rhythm.

After initial predictive cues have stimulated the developmental phase, local predictive cues become important and provide supplementary information concerning current conditions (Ramenofsky and Wingfield, 2007; Wingfield and Silverin, 2002). Examples include: temperature, rainfall, geomagnetic field, wind speed and direction, resource availability, social interactions, and specifics about the habitat (Kullberg et al., 2007; Ramenofsky et al., 2008; Richardson, 1990; Wingfield and Ramenofsky, 2011). Local predictive cues either accelerate or decelerate migratory functions, allowing the individual to more accurately adjust or synchronize behavior and physiology to the current conditions. Environmental conditions often differ between autumn and spring migrations, as do the responses of migrants to such cues.

Field and laboratory studies confirm that environmental temperature can modify behavior and physiology of migrants. Temperature probably influences the timing of autumn migration indirectly through influences on breeding and pre-basic molt by affecting food and water availability. A combination of warm and dry conditions can bring a precipitous end to breeding (Cain and Lien, 1985) and result in early molt and autumn departure in many species (Sokolov et al., 1999). In spring, warm temperatures can induce earlier departure dates from winter sites for free-living birds (Lack, 1960) or earlier onset of *Zugunruhe* in captives (King and Farner, 1963). Temperature also was found to influence fat deposition and mass gain in female white-crowned sparrows following photostimulation (Wingfield et al., 1996). Warm temperatures enhanced and cold temperatures limited mass gain in females but males showed no such adjustments. Such disparate effects probably reflect strong selective pressure on males to ignore such cues and arrive early on the breeding grounds to establish territories. Females, on the other hand, travel at a more conservative rate and arrive after males (Hunt et al., 1995; Morton, 2002b; Wingfield and Farner, 1978a,b; Wingfield and Hunt, 2002).

Date of first arrival at stopover sites and breeding areas can be consistent from year to year for some species (Morton and Pereyra, 1987); but see (Cotton, 2003; Hedenstrom et al., 2007; Jenni and Kery, 2003). However, rate of travel and tenure of birds recorded at stopover sites indicate that spring movements are more

synchronized and rapid than those of autumn in many species (Borrer, 1948; Cherry, 1982; King et al., 1963; King and Mewaldt; Morton and Pereyra, 1987; Stack and Harned, 1944). Spring migration is, therefore, considered to be more driven and rapid than the fall stage, which is often more facultative. Local conditions in autumn affect most migratory functions (e.g., rate of fattening, timing of departure from the breeding ground or stopover sites, termination, and decisions of whether or not to migrate in partial migrants (Jenni and Schaub, 2003)). Subordinate status in competitive encounters over food was associated with greater expression of migratory restlessness in captive dark-eyed juncos, which could be interpreted either as attempts to escape or continued migration (Terrill, 1987). The latter is supported by geographical separation of age and sex classes in free-living, wintering dark-eyed juncos: adult females and juveniles typically migrate further south in autumn to avoid direct competition over food with males (Ketterson and Nolan, 1982). Male dominance over females in the winter is not universal in migrant songbirds (e.g., Chaine et al., 2011), but winter dominance in male dark-eyed juncos may be selectively advantageous if wintering further north allows for earlier establishment of breeding territories. Low food availability, as well as cold weather, was also found to extend autumn movements of free-living Yellow-rumped Warblers (*Dendroica acoronata*) and Tree Sparrows (*Spizella pusilla*) Niles et al., 1969; Pulliam and Parker, 1979; Terrill and Ohmart, 1984. Further, severe weather conditions prolonged autumn migration for juvenile European Starlings (*Sturnus vulgaris*); whereas a mild autumn was associated with earlier cessation of migration (Perdeck, 1964). These dynamic systems demonstrate the variable selective pressures influencing the regulation of migration and suggest that local conditions can significantly influence the duration of mature expression in autumn migrants (Fig. 1).

3. Fueling

Migratory fat deposition, a key component of preparation for migration, is promoted by increased food intake (hyperphagia) and a higher digestibility (Bairlein, 2002), which precedes mass gain in studies of captive birds (Fig. 2). The dynamics of the relationship between food intake and body mass changes are complicated by the fact that the reproductive system is also developing, and also that there may be concurrent changes in energy expenditure, particularly relating to migratory locomotor activity. Migratory hyperphagia and fat deposition are photoperiodically regulated, with a spring phenotype being induced by a shift from short to long days (King and Farner, 1956; Koch and De Bont, 1952; Wolfson, 1952)(Fig. 2). The photoperiodic control of hyperphagia and fattening shares much in common with that of seasonal reproduction, with photoperiod providing initial predictive information (Wingfield, 2004). However, it is a matter of debate as to exactly whether photoperiod acts as a direct driver of seasonal cycles or as a synchronizer of endogenous circannual rhythms (Dawson, 2007; Gwinner, 1996). In contrast to spring fattening, little is known about the environmental control of autumnal fat deposition. It has been best studied in Gambel's white-crowned sparrows where fattening appears to be internally coupled to the expression of gonadal regression and pre-basic molt, and is induced as a remote effect of long day stimulation accelerated by decreasing day-lengths (King et al., 1963; Moore et al., 1982). However, most studies of captive migrants are performed on spring migration because it can be induced more predictably by shifting from short to long photoperiods.

Migratory fattening involves photoperiodically-regulated adjustment of the level around which food intake and body mass are maintained and defended. For example, Gambel's

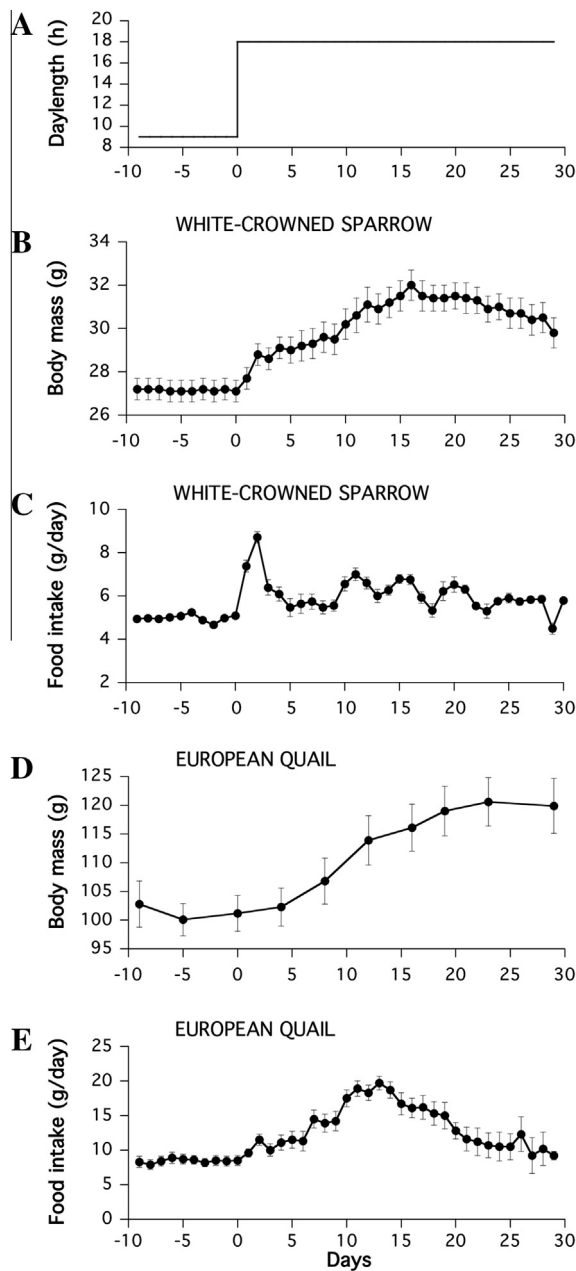


Fig. 2. Changes in daily food intake and body mass following photostimulation. Male Gambel's white-crowned sparrows (B,C) and European quail (D,E) showed increased body mass (g) and food intake (g/day) when transferred from short to long days (A). Data shown are means \pm SEM for each species ($n = 8$ white-crowned sparrow; $n = 7$ European quail; Boswell unpublished data).

white-crowned sparrows were fasted over several days during spring and autumn fattening and also during winter so that they lost body mass and were subsequently allowed to re-feed (King et al., 1963). The body mass re-attained by previously-fasted birds during migratory fattening was greater than that during winter and corresponded to the seasonally appropriate level maintained in control birds that had not been fasted. The results, comparable with findings in garden warblers (*Sylvia borin*) (Berthold, 1975) and in seasonal mammals, support the existence of a 'sliding set point' for body mass, or 'programmed rheostasis' (Mrosovsky, 1990), with an increase in the regulated level being associated with migratory fat deposition. Thus, there are two distinct sets of physiological mechanisms that regulate body energy stores in mi-

grants: rheostatic mechanisms set body mass at a seasonally appropriate level, and homeostatic mechanisms operate to ensure that the seasonal 'set point' is re-attained after energy stores have been lost following an energetic challenge.

The activation of homeostatic mechanisms is particularly important for replenishing fuel supplies once migratory flight has been initiated and birds undergo cycles of fasting and feeding as they alternate between long flights and stopovers. More is known in vertebrates about the homeostatic regulation of body mass than rheostatic regulation and, in mammals, the arcuate nucleus of the hypothalamus is a key homeostatic regulatory center (Boswell, 2010; Sawchenko, 1998). One group of neurons in this nucleus synthesizes neuropeptide Y (NPY) and agouti-related protein (AGRP), both of which stimulate food intake and promote mass gain. These neurons are interconnected with another cell group that expresses the pro-opiomelanocortin (POMC) and cocaine- and amphetamine-regulated transcript (CART) genes, the protein products of which (α -MSH in the case of POMC) reduce feeding and cause mass loss. As the arcuate nucleus lies outside the blood-brain barrier, it is readily accessible by blood-borne nutrients and metabolites as well as metabolic hormones, and the neurons express receptors for leptin, insulin, ghrelin and glucocorticoids. During an energetic challenge (e.g., experimental food deprivation), decreased circulating concentrations of leptin and insulin, and increased ghrelin and glucocorticoids promote increased synthesis and secretion of NPY and AGRP (and decreased or unaltered expression of POMC and CART). NPY and AGRP peptides act to restore lost energy stores when food becomes available by stimulating food intake, decreasing thermogenesis, and promoting fat deposition. Investigations in domesticated Japanese quail (*Coturnix japonica*) and migratory European quail (*Coturnix coturnix*) have revealed that the neuronal network in the arcuate nucleus (previously known in birds as the infundibular nucleus) has been conserved in birds, in terms of the neuroanatomical sites of expression of AGRP, NPY and POMC, co-expression of NPY and AGRP within the same individual neurons, and regulation of their mRNA levels by experimental food deprivation (Boswell et al., 2002; Phillips-Singh et al., 2003) (Boswell, unpublished data). Also, NPY stimulates food intake after administration into the brain of Gambel's white-crowned sparrows, both on long and short days (Richardson et al., 1995). Activation of NPY and AGRP neurons may be particularly significant in migratory birds in promoting the behavioral and physiological adjustments that are made at stopover sites to replenish energy stores that have been lost following migratory flights.

Measurement during stopovers of the metabolic hormones that regulate NPY and AGRP gene expression is a potential area for investigation but is complicated by the fact that there appear to be significant differences in the regulation of energy balance by metabolic hormones between birds and mammals. For example, the action of leptin in inhibiting NPY/AGRP cell groups and stimulating POMC/CART cell groups has been a major focus of research attention in mammals, but the leptin gene appears to be absent from the chicken and zebra finch genomes and its existence in birds is controversial (Friedman-Einat et al., 1999; Pitel et al., 2010). There is good evidence, however, for the existence of avian leptin receptors, and the chicken leptin receptor has been incorporated into a reporter system bioassay in cultured cells (Hen et al., 2008; Ohkubo and Adachi, 2008). The bioassay readily detected leptin bioactivity in mammalian serum samples but not in those from poultry. Similar observations were made when serum taken from bar-tailed godwits (*Limosa lapponica taymyrensis*) during migratory fattening was compared with human serum (Yosefi et al., 2010). This indicates that even if leptin is present in birds, the protein circulates at much lower concentrations in avian blood compared to mammals, or may have an autocrine/paracrine function. The lack of evidence in the bird choroid plexus (one of the

sites of transport from the blood into the brain) for a short isoform of the leptin receptor that is equivalent to that involved in leptin transport into the mammalian brain supports an autocrine/paracrine function (Liu et al., 2007). Leptin bioactivity can be demonstrated after experimental administration of mammalian leptin because leptin receptors are expressed in birds, as reported, for example, in migratory white-throated sparrows (*Zonotrichia albicollis*) (Cerasale et al., 2011). However, until an avian ligand for the leptin receptor is unequivocally identified, such findings must be interpreted with caution. The ghrelin signaling system also appears to be organized differently in birds because experimentally administered ghrelin tends to decrease food intake, contrasting with the stimulatory effects observed in mammals (Kaiya et al., 2009). However, fasting in domesticated Japanese quail increased plasma ghrelin concentrations, similar to mammals (Shousha et al., 2005). Thus it is possible that plasma ghrelin may reflect nutritional state in migratory species. Given the importance of lipids as a fuel source for migratory flight, it should also be investigated whether lipids and their metabolites are able to regulate the expression of arcuate nucleus neuropeptides directly.

The neural network in the arcuate nucleus is likely to play an important role in the homeostasis of body mass in migrants by coordinating the replacement of lost energy stores after energetic challenges such as migratory flight. The brain mechanisms promoting rheostatic increase in the defended level of body mass during migratory fattening, however, are not yet understood. One hypothesis is that seasonal changes in body mass are driven by coordinated alterations in the basal level of expression of arcuate nucleus peptides, so that mass increase is linked to increased basal expression of the anabolic NPY and AGRP genes as well as decreased or unaltered change in expression of the catabolic POMC and CART genes. In migrants, there is a possibility that seasonally-increased gene expression of NPY and AGRP is regulated by increased expression of the low-affinity glucocorticoid receptor by the NPY/AGRP neurons. In Gambel's white-crowned sparrows and red knots (*Calidris canutus islandica*), peripheral administration of the genomic low-affinity glucocorticoid receptor antagonist RU486 suppressed food intake and foraging behavior during the spring migratory phase, but did not affect food intake in wintering birds (Landys et al., 2004a,b). In mammals, the low-affinity glucocorticoid receptor is expressed by NPY/AGRP neurons and glucocorticoids stimulate NPY and AGRP gene expression (Briski et al., 2010; Shimizu et al., 2008). Work is needed to establish whether this is the case in migrants and, if so, whether expression of the low-affinity glucocorticoid receptor is up-regulated during spring migratory hyperphagia. One study in migratory birds has examined arcuate nucleus neuropeptide gene expression during spring migratory fattening (Boswell, unpublished data). In European quail sampled after 5 days' photostimulation, when body mass and food intake were significantly increased, it was predicted that NPY and AGRP expression in dissected basal hypothalamus (containing the arcuate nucleus) would be significantly increased and POMC expression decreased or unchanged compared to lean short day controls, and also compared to phenotypic variant control birds that did not show photo-induced fattening. VIP (vasoactive intestinal polypeptide) gene expression was also measured because its RNA levels in the basal hypothalamus were significantly decreased after a 24-h fast in European quail (Boswell, unpublished data), as would be expected from the inhibitory effects of the peptide on food intake after central administration in domestic chicks (Tachibana et al., 2003). Therefore, decreased or unchanged VIP expression would be expected during seasonal fattening. The experimental findings did not support the idea that migratory hyperphagia and fattening are driven by co-ordinated changes in neuropeptide expression because AGRP and POMC expression were unchanged, while NPY and VIP mRNAs changed in the oppo-

site direction than predicted, being respectively decreased and increased. These findings are limited in that they are based on a single time-point in a single migratory species, so more work in other species is required to test the hypothesis further. However, the findings are supported by studies of seasonal mammals in which seasonal changes in body mass are not well correlated with the level of basal expression of arcuate nucleus neuropeptide genes (Jethwa et al., 2010; Morgan et al., 2003). The significant increase in VIP mRNA observed in relation to migratory fattening in the European quail is of interest. Kuenzel and Bläher (1993) proposed that VIP plays an important signaling role in an avian 'visceral fore-brain system' (a series of neural connections proposed to regulate cardiovascular, respiratory and gastrointestinal processes). This system would theoretically regulate the expression of seasonal events such as migratory hyperphagia and fat deposition by altering the balance of activity between the sympathetic and parasympathetic branches of the autonomic nervous system.

Given the importance of photoperiod as an environmental regulator of migratory hyperphagia and fattening, body mass rheostasis must interact with the brain mechanisms controlling seasonal photoperiodic signaling. These are best understood for the regulation of seasonal reproduction in domesticated Japanese quail and involve a signaling network between deep-brain photoreceptors, clock genes, and conversion within the hypothalamus of thyroxine (T4) into triiodothyronine (T3) following photo-induced release of thyroid-stimulating hormone (TSH) from the pars tuberalis of the pituitary gland (Nakane and Yoshimura, 2010). Little is known about how seasonal events other than reproduction are induced. One hypothesis is that the photoperiodic regulation of body mass shares common pathways with reproduction, and that local production of T3 acts within the brain to cause rheostatic adjustment of food intake and body mass during the migratory period. In Siberian hamsters (*Phodopus sungorus*), experimental implantation of T3 into the hypothalamus of animals on short days induced changes in body mass characteristic of a long-day phenotype (Murphy and Ebling, 2011). It is also noteworthy that changes in the ratio of circulating plasma T3–T4 have been linked to the regulation of migratory fattening and nocturnal activity in the redheaded bunting (*Emberiza bruniceps*) (Pathak and Chandola, 1982). An alternative idea is that different photoreceptor populations control the photoinduction of reproduction and body mass through distinct signaling pathways. This latter possibility is supported by the fact that more than one photopigment gene has been linked to the photoperiodic control of reproduction in birds (Davies et al., 2012; Ohuchi et al., 2012), and also that reproduction and migratory fat deposition may be under the control of different circadian oscillators (Kumar et al., 2006). More investigation in birds is required into the regulation of photoperiodically regulated processes other than reproduction to distinguish between these hypotheses. The steps involved in the photoperiodic cascade between reception of a photoperiodic signal and the expression of migratory hyperphagia are therefore unknown.

4. Departure

Departure occurs following the fueling stage of migration and is a complex decision requiring the synthesis of both endogenous and exogenous information. Local predictive information (e.g., barometric pressure, rain, wind, temperature etc.) is combined with information concerning intrinsic migratory state (e.g., motivation, physiological state, etc.) to affect departure decisions in many migrants (Jenni and Schaub, 2003; Newton, 2008). These types of inputs probably influence departure differentially depending on the type of migratory movement (e.g., long vs short distance, overland vs barrier-crossing, facultative vs obligate, etc.), the seasonal

context of the movement (e.g., vernal vs autumnal) and how late in the migratory season the flight is being made. As described in the previous section, one of the largest reorganizations of physiology that is common to most migratory events is in body composition via the process of fueling. It is a generally accepted hypothesis that departure occurs soon after an individual has accumulated sufficient energy stores for the anticipated flight and when the environmental or social conditions are permissive for flight (Berthold, 2001; Dingle, 1996; Jenni and Schaub, 2003; Newton, 2008). Fat deposits, for example, predict departure date for autumnal migration in mountain white-crowned sparrows (Morton, 2002b) and affect orientation behavior in robins (*Erithacus rubecula*) (Sandberg, 1994), chaffinches (*Fringilla coelebs*) (Backman et al., 1997) and red-eyed vireos (*Vireo olivaceus*) (Sandberg and Moore, 1996). Further, energy reserves predict stopover durations in garden warblers (*Sylvia borin*), whinchats (*Saxicola rubetra*), whitethroats (*Sylvia communis*) and several species of thrush en route (Fusani et al., 2009; Goymann et al., 2010; Yong and Moore, 1993). A link between energy accumulation and departure has motivated studies concerning metabolic hormones and their possible role in departure decisions, particularly for corticosterone, prolactin and leptin. While none of these hormones independently regulate departure decisions, it is possible that they have a permissive role or otherwise influence the probability of departure.

Corticosterone, a major avian glucocorticoid central to metabolism and the response to stress, is important in life cycle transitions of birds involving an increase in physical activity and unpredictability (e.g., Belthoff and Dufty, 1998; Breuner et al., 1998; Corbel and Groscolas, 2008; Heath, 1997; Silverin, 1997; but see also (Romero et al., 2006). Effects of corticosterone on activity are pronounced when coupled with an energy challenge (Astheimer et al., 1992), suggesting that corticosterone may play a large role in departure decisions for facultative movements (Wingfield, 1992). For example, corticosterone is thought to mediate altitudinal migratory behavior in white-crowned sparrows during snowstorms (see Section 6 for a detailed discussion; (Breuner et al., 2003) and the red crossbill, an irruptive migrant, shows synchronous elevation of baseline corticosterone and diurnal activity in response to food reductions in captivity (Cornelius et al., 2010). In the latter case, corticosterone secretion and behavioral response to food reduction were sensitive to social information, such that the response to food reduction was dampened if well-fed neighbors were nearby (Cornelius et al., 2010). Social information is probably a potent cue in facultative migrations where individuals are responding to real time changes in conditions (Chan, 1994). Corticosterone, therefore, remains a strong candidate as a mediator of departure decisions in facultative movements.

Seasonal migrations are more predictable and may, therefore, rely less on hormonal responses to local conditions for departure decisions. Studies in seasonal migrants, however, indicate that adrenal activity increases just prior to or during migration (John, 1966; Naik and George, 1963; Peczeley, 1976). Correspondingly, corticosterone is elevated prior to departure and in conjunction with increasing fat stores or body mass in both captive and free-living migrants (Holberton, 1999; Holberton et al., 2008; Landys et al., 2004c; Landys-Ciannelli et al., 2002; Piersma and Ramenofsky, 1998; Piersma et al., 2000). In the partial migrant blue tit (*Cyanistes caeruleus*), migratory individuals have higher fecal corticosterone levels than their resident conspecifics (though fecal levels may be difficult to compare given changes in food intake, digestion and excretion during migration) (Nilsson and Sandell, 2009) and red-eyed vireos with high corticosterone levels show higher activity levels and more appropriate orientation behavior in orientation cages (Lohmus et al., 2003). Descriptive studies thus suggest that corticosterone secretion anticipates migratory flight, but it remains unlikely that corticosterone induces departure

directly. Exogenous corticosterone administered to premigratory chaffinches and white-throated sparrows resulted in increased migratory restlessness (Dolnik and Blyumental, 1967; Meier and Martin, 1971), but there is concern that these results may have been pharmacological in nature. While baseline corticosterone in captive garden warblers showed a diel rhythm during the autumn migratory phase, the peak occurred towards the end of the nocturnal flight phase rather than preceding it (Schwabl et al., 1991). Experimental inhibition of corticosterone secretion through dexamethasone treatment prevented fat deposition and slowed mass gain in photostimulated dark-eyed juncos, but did not significantly affect hyperphagia or *Zugunruhe* (Holberton et al., 2007). The GR antagonist RU486 similarly had no effect on migratory activity in captive red knots or white-crowned sparrows, although it did decrease foraging behavior in red knots (Landys et al., 2004a; Landys-Ciannelli et al., 2002). Further, many migrants had larger fat deposits and higher corticosterone levels in the spring than they did in the fall – when time constraints are typically reduced and conditions are less severe (O'Reilly and Wingfield, 1995). Evidence to date therefore suggests that corticosterone supports seasonal migratory movements largely through metabolic preparations and preparation for unpredictable conditions en route (see Section 5 for role of corticosterone during flight).

Less research is available for effects of other hormones on expression of migratory behavior and departure decisions. Nocturnal restlessness was absent in thyroidectomized captive redheaded buntings and was restored through exogenous administration of T₃ and T₄ (Pathak and Chandola, 1982). While the ratio of T₃–T₄ increased prior to spring migration in this study there was no such change in the autumn, suggesting complex or seasonally specific contributions to departure decisions. Prolactin also increases with photoperiod in the spring and is known to stimulate fattening and migratory behavior in some migrant species (Meier and Davis, 1967; Meier and Farner, 1964). In conjunction with exogenous corticosterone, prolactin was also found to induce migratory activity (but note possible pharmacological doses; (Meier and Martin, 1971). Interestingly, the time of injection was important in achieving these effects and it has been hypothesized that the phase relationship between prolactin and corticosterone underlie changes in migratory activity (Dusseau and Meier, 1971; Meier and Martin, 1971). In contrast with these findings, endogenous prolactin levels correlated well with photoperiod but not with development of migratory condition in European quail and administration of exogenous prolactin caused an increase in food intake rates regardless of the time of administration (Boswell et al., 1995). Holberton et al. (2008) detected increases in corticosterone and prolactin in photostimulated captive dark-eyed juncos, but neither hormone correlated with migratory restlessness nor fat deposits in a given sampling period.

Leptin has been proposed as a mediator of departure decisions given that it could be a reliable indicator of fat content and, thus, migratory readiness (Holberton et al., 2005). Seasonal or diel descriptions, however, are not yet possible given that the ligand for the leptin receptor has not yet been definitively isolated in birds (see Section 3). In any case, leptin receptor expression does not differ between the migrant and wintering phases in captive white-throated sparrows (Cerasale et al., 2011). Early investigations using exogenous murine (mouse) leptin, however, suggest that response to the ligand does vary in migrants: murine leptin resulted in decreased food intake and body mass in wintering birds but had no such effect in migrants (Cerasale et al., 2011). Migratory behavior (*Zugunruhe*) was not reported.

Departure involves a change in diel activity rhythms in nocturnal migrants – suggesting that melatonin may either be affected by or affects departure decisions. Melatonin profiles were indeed lower at night during migration than other times of the year in several

studies (Fusani and Gwinner, 1046; Helm et al., 2012, 1993). Notably, non-migrant birds displaying periodic or irregular nocturnal activity did not show these reduced melatonin levels (Fusani and Gwinner, 1046). Melatonin levels also increased and *Zugunruhe* was suppressed in captive migrant birds during fasting; however, the expression of *Zugunruhe* was more affected by food availability than by melatonin in garden warblers held overnight at a stopover location (Fusani et al., 2011; Fusani and Gwinner, 2004). These dynamics have been interpreted in several ways, including: (1) reduced melatonin during flight is an adaptation that allows for rapid adjustment to new photoperiods experienced en route (Gwinner et al., 1997), and (2) low melatonin during migratory flight reflects a high body temperature and metabolic rate (Wojciechowski and Pinshow, 2009). It may also be possible that melatonin is interacting with other hormones to affect nocturnal behavior. Tsutsui and colleagues discovered that 7 α -hydroxypregnenolone, a brain-derived steroid, stimulated locomotor behavior at night in Japanese quails that was inhibited by melatonin (Tsutsui et al., 2008). Pinelectomy increased expression of 7 α -hydroxypregnenolone and melatonin decreased it (Tsutsui et al., 2012). Interestingly, however, stimulatory effects of 7 α -hydroxypregnenolone on nocturnal behavior occurred only in males, offering confusion as to how or if this neurosteroid influences a behavior shared by both sexes.

In summary, there is no definitive evidence that a given hormone directly stimulates departure in migrant birds. It is plausible, however, that a suite of hormones provides information concerning endogenous condition to brain regions controlling migratory behavior and may influence departure decisions.

5. Flight

Migratory endurance flight differs from endurance locomotion of mammals in at least three respects (Jenni and Jenni-Eiermann, 1998; Jenni-Eiermann and Jenni, 2012). First it is performed at a very high metabolic rate. In contrast to walking, the relationship between speed and energy expenditure during flapping flight is U-shaped. A walking animal can slow down to reduce energy expenditure. A flying bird, however, cannot escape a certain level of power output, determined by the lowest point of the U-shaped power curve. Even at this minimum, the metabolic rate of flying birds is about twice the maximum rate of exercising small mammals and is among the highest in all vertebrates (Butler et al., 1998). Second, this high metabolic rate is maintained for hours (normally an entire night) and up to 100 h in certain species. Third, most bird species (except aerial feeders) do not feed or drink during endurance flight and, thus, have to rely exclusively on body stores of energy and water.

The power needed to carry additional weight in flight is much higher than when walking or swimming (Schmidt-Nielsen, 1984). Hence, it is of paramount importance that the energy density of stored fuel is high. Stored lipids have an energy density that is more than seven times that of glycogen and protein. Fat from adipose tissue yields eight times more chemical energy (e.g., ATP) than wet protein, and 8.2–10.3 times more than glycogen (Jenni and Jenni-Eiermann, 1998). This is chiefly because fat stored in adipose tissue contains only about 5% water (Piersma, 1997), compared with 70% or more for muscle tissue or stored glycogen. Another advantage of adipose tissue is its comparatively low maintenance costs (Scott and Evans, 1992). However, lipids are stored mainly extra-muscularly in birds, requiring mobilization from adipose tissue and transportation as free fatty acids (FA) by soluble protein carriers to the mitochondria of the flight muscles (McWilliams et al., 2004). Although FA transport is rate limiting during oxidation in mammals (Weber, 1992), it may be circumvented in passerines by a lipoprotein-mediated pathway and by up-regula-

tion of transport proteins. Actively migrating birds caught out of flight had very high levels of triglycerides and very-low-density-lipoproteins (VLDL) (Jenni-Eiermann and Jenni, 1992). It was suggested that fatty acids could be taken up by the liver as well as by flight muscles, where they would be re-esterified and released into the plasma as VLDL. This conversion would allow large fluxes of fatty acids to the flight muscles without increasing plasma viscosity and would circumvent the limitations set by albumin to fatty acid transport. Elevated triglycerides and VLDL have not, however, been observed in other species sampled under experimental flight conditions (Jenni-Eiermann et al., 2002; Pierce et al., 2005; Schwilch et al., 1996). FA is then transported into the cell and across the cell membranes by heart-type fatty acid binding protein (FAT/CD36 and FABPm) and in the cytosol (H-FABP). These transport proteins are up-regulated during the migratory season by up to 70% (Guglielmo, 2010; Guglielmo et al., 2002, 1998; McFarlan et al., 2009; Pelters et al., 1999).

FA cannot, however, cover all of the fuel needs during migration. During migratory flight proteins are catabolized as a complement to lipids for various reasons (Jenni and Jenni-Eiermann, 1998; Jenni-Eiermann and Jenni, 2012), including: to supplement endogenous protein turnover and repair (Guglielmo et al., 2001), to provide gluconeogenic precursors, to refill citric acid cycle intermediates (anaplerotic flux) for oxidation of fatty acids, and to provide water. Finally, body mass and, thereby, the power and muscle mass required for flight, continually declines as fuels are depleted during a long flight. Catabolizing flight muscles may, therefore, allow for continual adaptation that maximizes fuel vs load efficiency (Pennycuik, 1998). Carbohydrates, stored mainly in the form of glycogen in the liver and skeletal muscles, cannot quantitatively serve as a fuel complementing lipids during endurance flight. Experiments with pigeons have shown that within one hour the intracellular glycogen reserves of the white fibers were completely depleted (George and Nene, 1965; Rothe et al., 1987).

The optimal composition of fuel types for migratory endurance flight thus appears to be a maximum of lipids and a minimum of protein. Endurance flight of birds is fuelled with the same contribution of energy derived from protein (i.e. about 5% in fat birds) and lipids (about 95%) as during fasting at rest (Fig. 3; see also (Vailancourt et al., 2005) for running birds). This pattern is particularly interesting since endurance flight is performed at 60–85% VO_2 max, or more when birds are loaded with fuel (Guglielmo et al., 2002). In comparison, mammals (including humans) rely to a smaller extent on lipids during strenuous endurance exercise (e.g. 40–50% in marathon runners, (Callow et al., 1986) and the relative contribution of energy derived from fat during fasting is even lower and decreases when energy expenditure approaches its maximum (VO_2 max)) (Guglielmo, 2010; Roberts et al., 1996). Only when walking do exogenous fatty acids provide most of the energy in mammals (Roberts et al., 1996). If an energy contribution of 95% fat and 5% protein are transformed into live bird mass, the energy reserves should be composed of 70% fat and 30% protein, largely because of the high water content of protein and therefore the relative low energy yield per g wet mass. The comparatively small contribution of 5% energy from protein thus requires 30% of additional weight to carry in flight. So, in summary, protein catabolism is a costly requirement for long-distance flight.

Coordinating mechanisms must exist to achieve an adaptive balance between lipid and protein catabolism throughout flight. Corticosterone may be involved in the regulation of metabolism during flight and the composition of fuel types used (Jenni et al., 2000). Elevated levels of corticosterone promote gluconeogenesis from amino acids and, thus, increase breakdown of muscle protein (Gwinner et al., 1992; Kettelhut et al., 1988). Studies in free-living small passerines caught during migratory flight

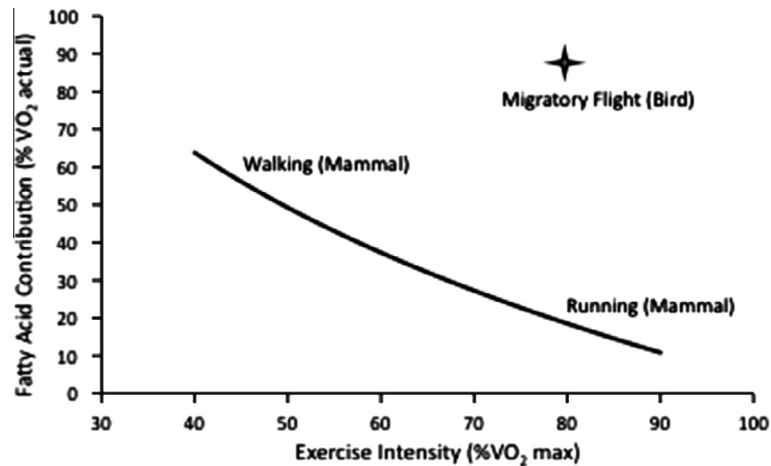


Fig. 3. Migratory birds rely more heavily on fatty acid as an energy source during intense exercise than do mammals. As exercise intensity increases, mammals (black line) depend less on FA as a fuel source, whereas nearly 95% of the energy used by migratory birds (star) operating at 80% VO₂max comes from fatty acids. Redrawn from Guglielmo (2010).

(Falsone et al., 2009), in homing pigeons after a 180 km flight (Haase et al., 1986), and in shorebirds just after landing from a long spring migratory flight (Landys-Ciannelli et al., 2002; Reneerkens et al., 2002) showed slightly increased, intermediate corticosterone levels in comparison with resting birds. These data support the hypothesis of an up-regulation of corticosterone as a response to increased energy demands. However, in laboratory studies results were equivocal showing either slightly increased corticosterone levels (ducks and pigeons exercising in a treadmill; (Harvey and Phillips, 1982; Rees and Harvey, 1987) or unchanged levels (pigeons electrically stimulated for 2 h, (John and George, 1973); red knots flying in a wind tunnel for 2 and 10 h, respectively, (Jenni-Eiermann et al., 2009). Whether the latter results might be explained by the experimental situation remains to be shown. In any case, corticosterone increases to variable degrees during flight, but only rises to the very high concentrations typical of an acute stressor when fat depots are nearly depleted and birds in endurance flight enter phase III of fasting (Gwinner et al., 1992; Jenni et al., 2000). In this case, corticosterone seems to trigger protein catabolism as suggested by the emaciated breast muscles and the high uric acid levels in those individuals (Gwinner et al., 1992; Jenni et al., 2000).

The role of other hormones in the regulation of flight metabolism has been investigated in free-flying homing pigeons, but not in migrant birds. After a flight of 48 km or about 1.5 h, significant increases of glucagon, adrenaline, noradrenaline and growth hormone, and either significantly reduced or unchanged concentrations of T3 and T4 were found (George et al., 1989; John et al., 1988; Viswanathan et al., 1987). George et al. (1989) concluded that increased sympathetic activity increases glucagon, a lipid-mobilizing hormone. The inconsistent results for T3 and T4 might be explained by differing training protocols. Only the untrained pigeons showed a decrease for thyroid hormone, most probably as a consequence of the activation of the HPA-axis, which in turn reduces peripheral T3 formation and suppresses thyroidal T4 secretion (see (George et al., 1989) and citations therein).

In conclusion, migrating birds are unique in that they fuel endurance flight with the highest possible percentage of energy derived from fat oxidation. As a consequence their metabolism shows particular adaptations to push lipid mobilization, FA-transport and oxidation during flight to a maximum. It is therefore astonishing that the hormonal regulation of this extraordinary metabolism is largely unknown.

6. Arrival

Termination of migratory behavior upon arrival at a breeding or over-wintering site probably involves mechanisms of habitat imprinting, recognition and resource evaluation (Gwinner and Czeschlik, 1978; Hahn et al., 1995; Ketterson and Nolan, 1990). It is largely unknown how hormones contribute directly to the termination of migration, although they may play a role in the transition between the migratory and reproductive life cycle stages (see below). In future research it will be important to consider distinctions across seasonal stages and migratory strategies. Of further interest will be whether or not mechanisms (e.g., response to local predictive cues) that terminate migration are similar to those regulating migratory decisions in facultative migrants or suppression of migratory behavior in partial migrants.

When birds terminate migration and begin to breed there is a transitional phase defined by alternating or simultaneous expression of characteristics from both stages (Jc, 2008; Ramenofsky and Wingfield, 2006). Behavior and physiology during this transition [termed 'arrival biology' by Ramenofsky and Wingfield (2006)] must be highly flexible, especially in long distance migrants. Long distance migrants base the timing of migration on highly predictable cues, such as photoperiod, and so arrive at the breeding sites with little predictive power of when breeding will begin or what conditions they might face. Hence, local cues, such as snow pack, temperature, and conspecific cues can be very important in accelerating or inhibiting the onset of breeding once the migrant arrives.

Glucocorticoids (GCs) are a likely candidate for the transduction of environmental cues into behavioral and physiological change associated with this process (Wingfield and Ramenofsky, 1997). GCs integrate environmental information and then promote physiological and behavioral change appropriate to the situation. Across life history stages GCs are thought to enhance survival probabilities at the expense of reproduction. That is, when environmental conditions deteriorate, due to inclement weather, increased predation pressure, or increased social pressure, GCs redirect energy allocation away from non-essential functions such as reproduction and growth, and focus energy on self-maintenance, survival oriented activities (Wingfield et al., 1998; Wingfield and Sapolsky, 2003).

Within the migration/breeding transition, therefore, GCs may act to inhibit the progression into breeding if conditions at the breeding site are not yet appropriate for nesting. This hypothesis



Fig. 4. Environmental conditions and date of first egg lay at Tioga Pass. Yearly variation in conditions can be extreme in the high sierra, as exemplified by pictures of Lee Vining Creek on June 7th, 1997 (A) and June 7th, 1998 (B). Date of first egg lay is significantly related to snow cover on Tioga Pass Meadow (C). Each point represents one year between 1995 and 2006. Redrawn from Hahn et al. (2004a), with 2002–2006 data added; 2000 and 2005 not shown for lack of snow cover data.

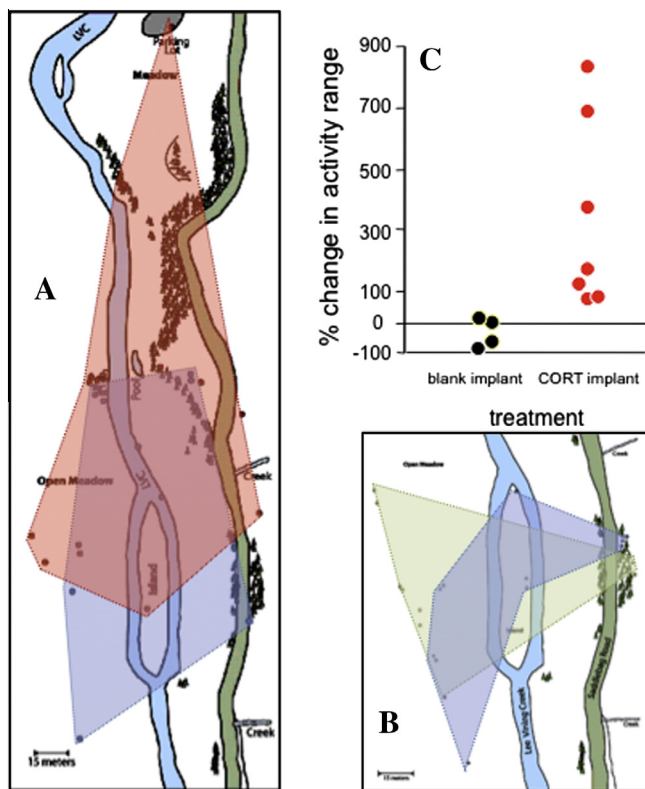


Fig. 5. Corticosterone increases activity range in pre-nesting white-crowned sparrows. Map A demonstrates an increase in activity range following CORT implant (blue pre-implant; red post-implant). Map B demonstrates a minimal difference in activity range following blank implant (blue pre-implant; green post-implant). The percent change in activity range (C) for all CORT individuals (red circles) is higher than in control-implanted individuals (black circles). Redrawn from Breuner and Hahn (2003a).

is supported by studies demonstrating that inclement weather can induce elevations in plasma corticosterone of white-crowned sparrows (Wingfield, 1983) and that migrant red knots arriving at the breeding grounds have high baseline corticosterone levels that decline only after individuals commence breeding (Reneerkens et al., 2002). In another study, pied flycatchers (*Ficedula hypoleuca*) arriving earlier to the breeding grounds had higher baseline corticosterone than those arriving later, suggesting either that a faster migration yielded a higher allostatic load or that conditions earlier in the spring required higher baseline corticosterone levels (Lobato et al., 2010). It is probable that species-specific life history and in-

ter-annual variation in conditions heavily influence the dynamics of corticosterone as it relates to arrival biology. Long-term studies are valuable in this regard in their ability to detect patterns that transcend inter-annual variability. Here we present data from a long-term study investigating environment–hormone–behavior interactions within the arrival phase of an intermediate distance migrant, the mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*).

The MWCS winters in Mexico, and breeds in sub-alpine meadows across the western United States (Cortopassi and Mewaldt, 1965). The focal population breeds at Tioga Meadow, just outside Yosemite Park in the Eastern Sierra (37°50'N, 119°10'W; 3030 m elevation). This population has been studied continuously since 1968: originally by Morton and more recently by Hahn and Breuner. This population is, therefore, the most-highly studied population of one of the most-studied wild passerines in the world. Male MWCS arrive at the breeding ground first, in early May, with females following around 2 weeks later (Hahn et al., 2004b; Morton, 2002a). When males first arrive at the breeding ground, there is often still complete snow cover. MWCS prefer to breed on the ground within the large willows (*Salix* spp); hence, at arrival, the majority of nesting sites are still buried under snow. The rate of nest-site emergence varies greatly year-to-year depending on residual winter snowpack and frequency or intensity of spring snow events. Fig. 4 demonstrates this variability with photos of the same location taken on June 7th in 1997 (a year of medium snow pack and mild weather in May) and June 7th 1998 (a year of high snowpack and extreme inclement weather during May). This variation in environmental conditions can have significant effects on reproductive timing (Morton, 1994). There is a strong relationship between the date when 50% snow cover was identified on the meadow and the date of first clutch initiation for the season (Fig. 4C; see Supplementary for description of methods). ML Morton has demonstrated a similar relationship between snow depth and the date of clutch initiation from 1968 to 1993 (Morton, 1994). Clearly, snow cover is strongly predictive of the timing of initiation of reproduction.

The arrival phase of the mountain white-crowned sparrow is thus marked by male arrival at the breeding site in early May when conditions are extreme, inclement weather is common, and the date of nest-site emergence is highly variable. These conditions require a high level of flexibility in the transition from migration to breeding by the sparrows. The following studies support the hypothesis that the HPA-axis helps to maintain a more facultative and irruptive state, expressed despite a high degree of territoriality, until conditions become permissive for nesting.

At arrival, males are localized over much of Tioga Pass Meadow. As the snow melts off and conditions improve, however, male activity range becomes narrower as territories are defined. We used radiotransmitters to investigate the role of corticosterone in

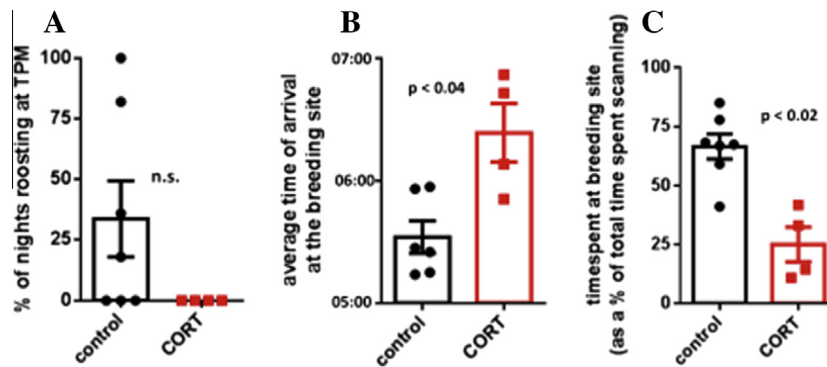


Fig. 6. Corticosterone implants extend time away from the breeding site during storms. No CORT-implanted birds roosted at the breeding site during storms, whereas some control birds did (A; note that treatment group averages were not significantly different). If a sparrow roosted at low elevation, the time of arrival at the breeding site the next morning was recorded. CORT-implanted birds arrived significantly later than blank-implanted control birds (B). Of the total time spent scanning for presence/absence at the breeding site, the percentage of time each individual was present was lower for CORT-implanted birds than it was for blank-implanted birds (C). Data shown are means \pm SEM of individuals in each treatment ($n = 7$ for control, black circles; $n = 4$ for CORT, red circles). Each dot represents the mean for an individual over the study. Mann–Whitney test used to determine significance across treatments. Redrawn from Breuner and Hahn (2003a).

activity range of males by localizing them repeatedly for several days before implanting corticosterone or blank silastic implants (Breuner and Hahn, 2003b). Blank implants caused no significant change in activity range, while every bird receiving a CORT implant (note that doses were physiological, Fig. S1) increased activity range (Fig. 5). As apparent in Fig. 5A, the increase in activity range was often the result of one or two localizations far outside the sparrow's normal range. Hence, it appears that CORT-implanted birds may be in a more irruptive state where they are more likely to leave the normal activity range if perturbations occur.

It is common for storms to cover the ground with a fresh layer of snow during the arrival phase. Early in the season the sparrows primarily eat insects that have blown up from lower elevations and are lying on top of the snow (Morton, 2002a). New snowfall can cover all available insects, bringing food availability at the breeding site close to zero. In response, the sparrows may choose to abandon the breeding site for lower elevation refugia. The Eastern Sierra is quite steep, allowing for birds to descend 500–1000 m elevation in just a few kilometers (Hahn et al., 2004b). The sparrows do not breed at these low elevation sites but remain there until conditions improve at the high elevation breeding grounds. Hahn et al. (2004a) and Breuner and Hahn (2003a) describe this behavior using radiotelemetry with both high and low elevation localizations during inclement weather. Birds descend to low elevation sites as conditions deteriorate and often roost at low elevation. The decision to stay at low elevation overnight appears to depend on temperatures at the breeding site the previous day (i.e., lower temperatures lead to higher likelihood of low elevation roosting (Hahn et al., 2004a). Individuals often return to the breeding site in the morning to sing for a few hours, and then either stay to roost at high elevation or return to low elevation (Breuner and Hahn, 2003a). This irruptive behavior may be an extension of the migratory state, where the birds return to the low elevation staging sites they used when first coming to the breeding grounds.

To explore the effects of corticosterone on this irruptive behavior, we placed radiotransmitters on birds and implanted them with either corticosterone or control silastic implants. This study took place during an extended series of storms in 1998, a year when snow pack was well above average (232 cm on April 1st compared to a 75 year average of 170 cm), and breeding was delayed several weeks beyond average nest initiation (Hahn et al., 2004b; Morton, 2002a). All birds in the study left the breeding site for lower elevation refugia during the 10 days following implantation. However, corticosterone implant significantly altered patterns of behavior as compared to control birds (Fig. 6). On average across all days,

~35% of control birds roosted at the breeding site, whereas none of the CORT implanted birds ever roosted at the breeding site (Fig. 6A). Additionally, individuals that had roosted at low elevation returned to the breeding site between 04:45 and 07:00 h, but corticosterone implants delayed the return by an average of 52 min (Fig. 6B). Finally, CORT-implanted birds stayed at the breeding site for less total time before returning to low elevation (Fig. 6C). Hence, corticosterone appears to favor the extension of a facultative, irruptive state over the initiation of breeding behavior.

In summary, MWCS must be flexible in the initiation of breeding on arrival at their high elevation breeding sites. This flexibility appears to manifest itself as an extension of irruptive staging behavior common to the end of the migratory life history stage. Evidence suggests that corticosterone promotes this extension by increasing irruptive movements outside of an animal's normal activity range during good weather and by increasing staging behavior at lower elevations away from the breeding site during inclement weather.

7. Conclusions

This review summarizes the current understanding of the environmental regulation of the migration life history and describes the endocrine mechanisms underlying the specific phases of the cycle. We hope to have emphasized here several main points. It is particularly beneficial to consider migration as a complex process containing multiple, distinct phases in order to fully understand the process and avoid confusion when making cross-species or study comparisons. Distinctions may exist between the regulatory control and expressions of spring and autumn stages and more comparative studies in this realm are needed. Although the field of avian migratory endocrinology is progressing, there is much we don't understand regarding the role of hormones in bird migration. There is a particular dearth of information concerning the autumnal migration and the flight phases of migration due mostly to methodological difficulties or technological limitations. We suspect that innovations in remote-tracking technology, proteomic/genomic and endocrine techniques, as well as continued manipulations of captive and free-living populations, will be particularly useful in filling these gaps of knowledge. Finally, we encourage continued efforts in descriptive, natural history studies given the importance of accurately describing the phenomenon we seek to understand.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ygcen.2013.03.027>.

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