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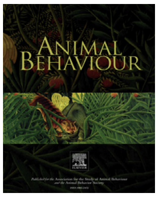

Special Issue: Mechanisms & Function

Regulation of complex behavioural transitions: migration to breeding

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The evolution of migration combines the selective advantages of breeding with ephemeral resources at high latitude or altitude with the benefits of overwintering at distant sites with adequate resources to promote survival. Migration between sites involves changes in behaviour, especially the transition from migration to nesting, or in autumn, the transition to wintering stage. We focus here on the vernal transition. Because migration and onset of nesting are mutually exclusive events, transition from a social, hyperphagic and highly mobile state to territoriality and pair bonding involves complex behavioural changes. In Arctic regions, weather in spring is unpredictable adding another dimension of complexity to the migration/breeding transition. Nevertheless, the brief Arctic summer requires that songbirds arrive on the breeding grounds while conditions may still be unfavourable, thus delaying nesting until conditions ameliorate. This requires flexibility and coordination of migration behaviour to be able to leave if weather deteriorates, or to become territorial, attract a mate and begin nesting within hours when conditions permit. In Gambel's white-crowned sparrows, *Zonotrichia leucophrys gambelii*, neuroendocrine regulation of reproductive development progresses throughout vernal migration so that males and females are mature when they arrive on the nesting grounds, but final ovarian maturation leading to ovulation and reproductive behaviours is suppressed. What provides the ‘brake’ to the onset of nesting? We focus on the adrenocortical response to acute stress that is greatly increased at arrival, especially in males, probably to enable flexibility in behavioural responses to severe weather. More recent evidence suggests that a hypothalamic peptide, gonadotropin-inhibiting hormone (GnIH) may provide the brake for the onset of nesting without suppressing development of a functional reproductive system. Experimental investigations show that gene silencing of GnIH in the brain increases singing and reproductive behaviours accompanying the onset of nesting. Thus we suggest that corticosteroids and GnIH play important regulatory roles specifically at the transition from vernal migration to the onset of nesting.

Avian species that breed in the Arctic are almost all migrants that spend the winter at lower latitudes (Dingle, 2014; Piersma, 1994; Pielou, 1994). On their return to the Arctic in spring, they are frequently faced with extreme conditions, including complete snow cover and temperatures well below freezing. Even in warmer springs, when snow cover is almost gone, the potential for further snow storms covering patchy food resources is very great. Despite these unpredictable conditions, arriving migrants need to locate a nesting area, establish territories and form pair bonds as early as possible and then initiate nesting activities when conditions are conducive for breeding to ensure the greatest reproductive success. However, they must also adjust their physiology and behaviour to withstand severe weather and sudden food shortages (O'Reilly & Wingfield, 1995; Wingfield & Hunt, 2002; Wingfield et al., 2004). Because blizzards and subfreezing weather can occur unpredictably at any time during the spring, summer and early autumn, migrant birds are faced with ‘trade-offs’ of needing to nest and ensure reproductive success or respond to severe local conditions favouring self-preservation to the detriment of reproductive success. Such trade-offs require rapid and complex transitions of behaviour and physiology, but the mechanisms underlying such mobile flexibility, even nomadism, followed by territorial and reproductive behaviour are only beginning to be understood.

On the North Slope of Alaska (66–71°N), snow may melt from the tundra as early as the first week in May, but subsequent storms (and temperatures down to −11 °C or lower) may inundate early migrants. In other years, snow and subfreezing temperatures may persist into late May and early June (Hahn, Wingfield, Mullen, & Deviche, 1995). Further north, as the coastal plain nears the Arctic Ocean, temperature fluctuations are less extreme, possibly due to

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the ameliorating effects of the ocean (Stieglitz, Dery, Romanovsky, & Osterkamp, 2003). The breeding season of passerines at the northern limit of their range is 3–4 weeks longer than at Toolik Lake Field Station about 160 km to the south. In other Arctic study areas (e.g. field sites at Thule in northwest Greenland, 76°N), at the northern edge of breeding grounds for songbirds, weather is even more severe, with some of the most truncated breeding seasons known (Wingfield et al., 2004). Taken together, there is growing evidence that flexible hormone–behaviour adaptations have evolved in Arctic-breeding birds to cope with unpredictable weather, patchy trophic resources and fluctuating numbers of predators, all of which vary not only with location in the Arctic, but also from year to year.

As the spring migrants approach breeding sites, flight paths become more dispersed (Emlen, Demong, Wiltschko, & Bergman, 1976), and birds frequently become locally nomadic searching for refuges with food patches and cover (Cornelius, Boswell, Jenni-Eiermann, Breuner, & Ramenofsky, 2013; Gwinner & Czeschlik, 1977; Wingfield & Hunt, 2002; Wingfield et al., 2004). This is especially true if severe weather conditions prevail. None the less, migrants must endure and eventually settle when habitats conducive to breeding become available (Romero & Wingfield, 2016; Wingfield et al., 2004). Nomadic movements tend to be prolonged in years of inclement weather (deep snow pack), but songbirds can quickly transition from arrival to settlement, territory formation and pair-bonding behaviour when nesting habitat becomes accessible. Not infrequently, later snow storms can blanket established territories and birds revert to nomadism once more to locate refuge and food patches (Breuner & Hahn, 2003; Wingfield et al., 2004). This may happen in response to severe weather events even after nesting has begun. Thus, the ability to switch back to nomadic movements, form loose foraging flocks and turn off territoriality and breeding is crucial for these high-latitude/altitude birds to survive capricious conditions and to maximize reproductive success (Astheimer, Buttemer, & Wingfield, 1995; Hahn et al., 1995).

How are these complex transitions of behaviour and physiology accomplished? Birds migrate seasonally and arrive at destinations in loose groups. Moving in small flocks may be important to coordinate communication, orientation, arrival and subsequent events. To quote Low (2014, page 210), ‘Birds that live on grain maximize food-finding and safety by usually roaming in groups, a habit that suits colonization (arrive alone and you can expect to die alone)’. The Arctic spring is short and unpredictable and coordination is important leading up to settlement, territoriality and pair bonding. As such, there appears to be facultative overlap of the final substages of migration with settlement and onset of breeding. Once settled and paired, commencement of nesting follows when resources are sufficient. However, flexibility in timing at this juncture is reduced because incubation length and time to fledge young are more fixed (Ramenofsky & Wingfield, 2006; Wingfield, 2008; Wingfield et al., 2004). Here we highlight complex transitions in behaviour and how they might be controlled from vernal migration to onset of nesting in Arctic-breeding songbirds.

MIGRATION TOWARD THE BREEDING GROUNDS

Gambel's white-crowned sparrow, *Zonotrichia leucophrys gambelii*, is a long-distance nocturnal migrant. It travels great distances between its Arctic breeding range and overwintering sites extending from the lower 48 states into Mexico. In captivity, *Z. l. gambelii* exhibit migratory behaviour and physiology characteristic of free-living birds that include hyperphagia, fattening and nocturnal locomotor activity, termed migratory restlessness or Zugunruhe, a representation of migratory flight in captive birds (Agatsuma & Ramenofsky, 2006; Ramenofsky et al., 2003; Ramenofsky & Németh, 2014). The endocrine control of vernal migration has been the subject of research for over 60 years, but the coordination of preparations for migration and stopover biology resulting in refuelling for the next flight remains unclear. Testosterone and prolactin are involved in the fattening process, and glucocorticoids and thyroid hormones are probably important for most vernal events (see Pérez, Furlow, Wingfield, & Ramenosky, 2016; Ramenofsky & Wingfield, 2006; Ramenofsky, 2011; Wingfield, Schwabl, & Mattocks, 1990). Here we focus on the hormonal bases of flexibility during the transition from migration to breeding rather than migration or reproduction specifically.

Next we review the evidence for a role of corticosterone during migratory flight. There is extensive evidence that baseline plasma levels of corticosterone are involved in metabolism (e.g. glucose and fatty acid management), foraging and locomotor activity associated with migration and facultative movements (Landys, Ramenofsky, & Wingfield, 2006; Ramenofsky, 2011; Romero & Wingfield, 2016; Sapolsky, Romero, & Munck, 2000). Consistent with these actions, elevated levels of plasma corticosterone have been documented in a variety of long-distance migrants when captured en route during autumn, at departure from stopover sites in spring, or on arrival at the breeding grounds (Falsone, Jenni-Eiermann, & Jenni, 2009; Landys-Ciannelli et al., 2002; Reneerkens, Morrison, Ramenofsky, Piersma, & Wingfield, 2002) as well as in captive birds expressing nocturnal migratory restlessness (Ramenofsky, Moffat, & Bentley, 2008). In captive *Z. l. gambelii* held on a long-day photoperiod (18:6 h light:dark cycle), a clear expression of a diel sequence of behaviours is evident (Agatsuma & Ramenofsky, 2006). Throughout the daylight hours (photophase), birds feed, rest and show general locomotor activity. During the final 2–3 h of the photophase, they enter a quiescent stage and remain completely still until onset of the dark or scotophase, at which time they commence migratory restlessness, including a bill-up position in which the bill points skyward (Agatsuma & Ramenofsky, 2006; Coverdill, Clark, Wingfield, & Ramenofsky, 2011; Landys, Wingfield, & Ramenofsky, 2004). At the scoto- to photophase transition, birds abruptly cease migratory restlessness, begin to feed and drink, and reduce locomotor activity. Plasma corticosterone levels track the onset and duration of migratory restlessness with a final peak at the scoto- to photophase transition (Landys et al., 2004; Ramenofsky et al., 2008) (Fig. 1a). By contrast, *Z. l. gambelii* held on winter or short-day photoperiods (LD 6:18 h) show neither a quiescent phase nor nocturnal migratory restlessness (Ramenofsky et al., 2003). They do however show a peak of corticosterone at the conclusion of the scotophase (Landys et al., 2004). Others have also identified diel rhythms of corticosterone in *Z. l. gambelii* held on both short-day and long-day photoperiods, with the peak occurring at the close of the scotophase (Breuner, Wingfield, & Romero, 1999; Landys et al., 2004) (Fig. 1b and c).

Such results raise the question of whether the diel patterns of corticosterone concentrations in blood are a function of dawn and dusk (lights on and off) rather than being specific to migratory restlessness and its termination at dawn. Previous studies showed that birds exposed to an extended scotophase (constant dim-light conditions) expressed continued migratory restlessness, suggesting that environmental conditions (night-time) may override or mask a daily cycle of locomotor activity (Coverdill, Bentley, & Ramenofsky, 2008). Thus, we asked whether plasma corticosterone would track the locomotor patterns and remain elevated throughout the extended period of migratory restlessness (Ramenofsky et al., 2008). First we verified the patterns of locomotor activity and baseline levels of corticosterone in spring migrants held on an LD 18:6 h photoperiod (Fig. 2a). Here again the pattern of elevated baseline corticosterone appeared throughout

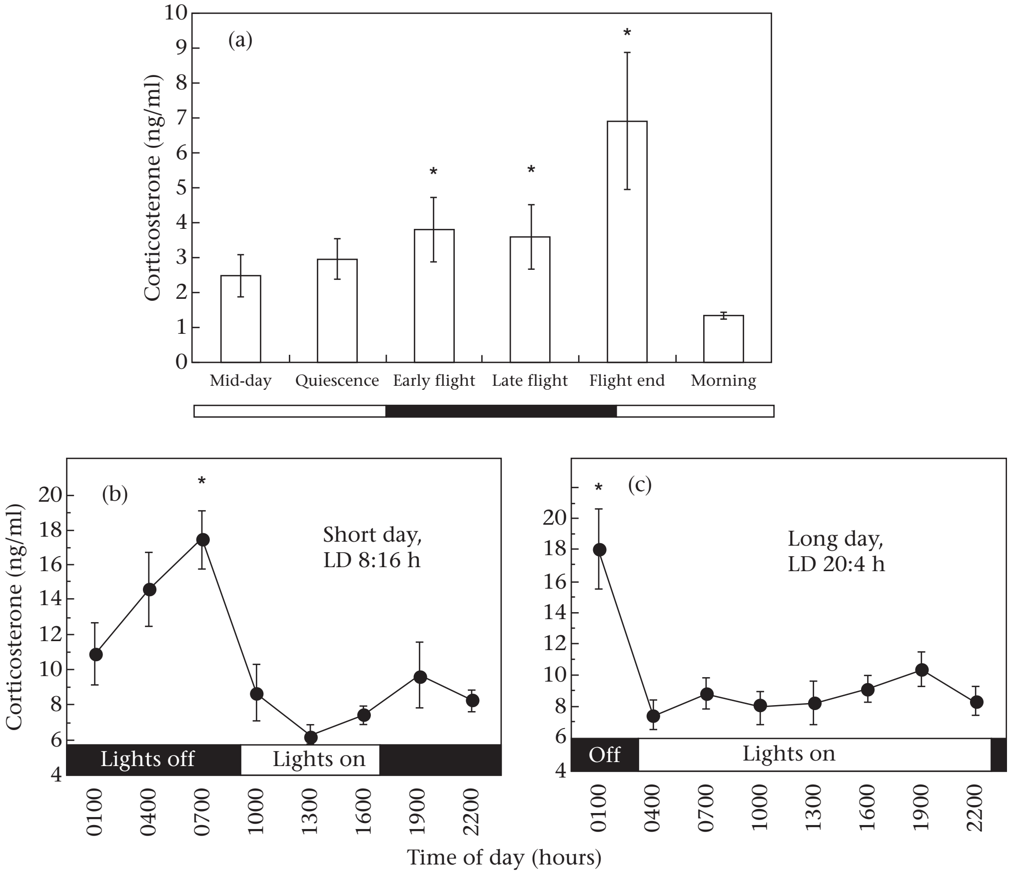

Figure 1. (a). Mean ± SE plasma levels of baseline corticosterone in captive migratory white-crowned sparrows ($N = 6$) on an 18:6 h light:dark cycle sampled at six periods characterized by specific behaviours: Mid-day, birds feeding and resting; Quiescence, birds immobile; Early flight, 2 h of scotophase, birds expressing migratory restlessness; Late flight, last 4 h of scotophase, with migratory restlessness; Flight end, onset of photophase; Morning, 2 h of photophase, low-level locomotor activity. Horizontal bars depict LD 18:6 h photoperiod: unfilled portion depicts photophase; filled portion depicts scotophase. An asterisk denotes a significant difference ($P < 0.05$) from the morning sample (from Ramenofsky et al., 2008, courtesy of ©Medimond S.r.l.). (b) Mean ± SE basal corticosterone levels in short-day sparrows ($N = 16$). An asterisk denotes a significant difference ($P < 0.0001$) from all 'lights on' values (from Breuner et al., 1999, courtesy of ©Wiley-Liss). (c) Mean ± SE basal corticosterone in long-day sparrows ($N = 16$, except at 2200 hours, where $N = 8$, and at 1300 hours, where $N = 14$). An asterisk denotes a significant difference ($P < 0.0001$) from all 'lights on' values (from Breuner et al., 1999, courtesy of ©Wiley-Liss).

the scotophase and peaked just at the transition to the photophase. Locomotor activity followed the daily patterns, with migratory restlessness apparent during the scotophase. In the final set of experiments, spring migrants initially held on an LD 18:6 h photoperiod and showing the normal pattern of migratory restlessness were then exposed to artificially extended scotophases by 8, 26 or 48 h (Ramenofsky et al., 2008). Extending the results of Coverdill et al. (2008), birds continued to express migratory restlessness throughout the prolonged scotophase while baseline levels of corticosterone remained elevated throughout (Ramenofsky et al., 2008; Fig. 2b). Therefore, it is likely that the sustained, elevated plasma levels of corticosterone during the extended scotophase are related more to the continuous energetic demands of migratory flight that masks the endogenous rhythm (Coverdill et al., 2008). These findings suggest that corticosterone may be acting at two levels. First, sustained plasma levels during the scotophase represent a facultative response to the increased demands, energetic and otherwise, of migratory restlessness. Second, the diel function showing a peak at the end of the scotophase acts at a level of greater amplitude, serving a preparatory function for daytime activity. Note also that the concentrations of corticosterone during migratory restlessness (or at night in general) are within the range of daily routines because stress levels after capture, handling and restraint are almost an order of magnitude higher (Fig. 2c). Therefore it appears that elevated corticosterone during extended migratory restlessness has some permissive/preparative role during migratory flight. This may also be advantageous for birds under severe environmental conditions requiring abrupt movements away from either a stopover or arrival destination.

These investigations also suggest that corticosterone may play an important permissive role in nomadic behaviour versus territorial and reproductive behaviours as loose flocks arrive to locate and settle on hospitable sites for breeding. Moreover, this permissive action may be critical later when nesting during periods of nomadism after a severe weather event interrupts breeding. These complex interchanges of activity in the face of high environmental unpredictability (see below) will be an important focus for future investigations and may provide insight into consequences of climate change and resultant increased frequency, duration and intensity of extreme weather events.

THE TRANSITION FROM MIGRATION TO ONSET OF BREEDING

As birds near their breeding grounds in the Arctic, migratory behaviour becomes less directed and the first reproductive behaviours start to be expressed. This period is characterized by a sequence of events, called 'arrival biology', that include arrival and

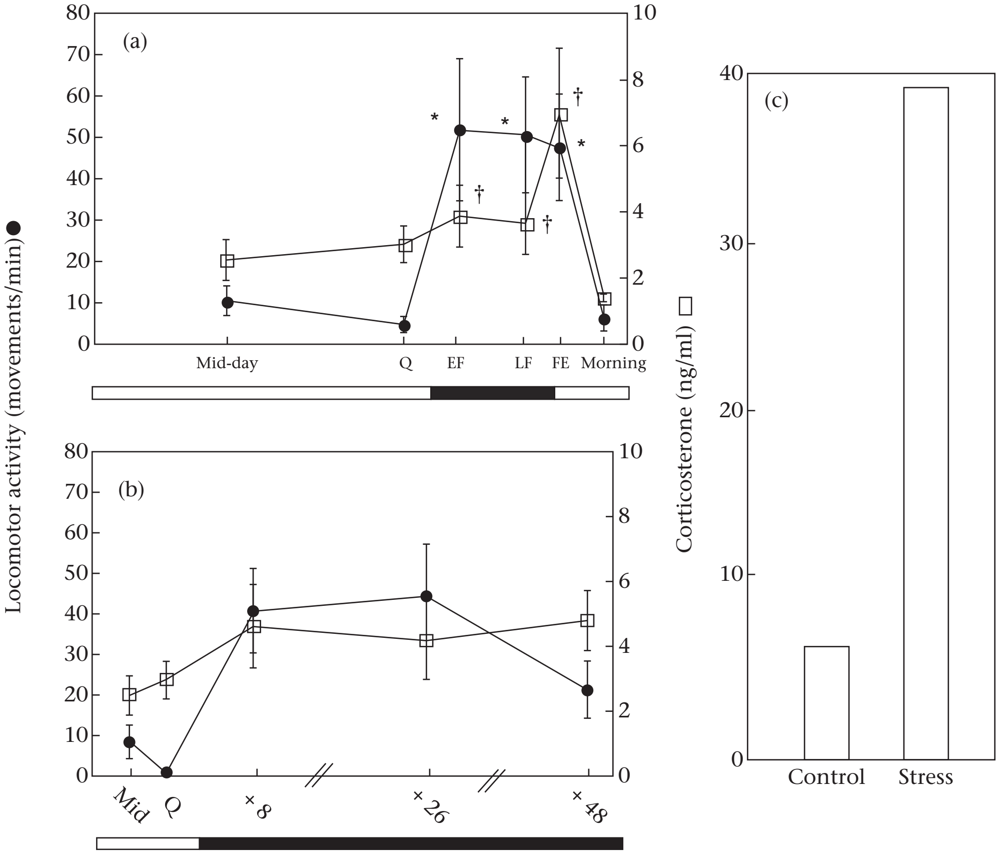

Figure 2. (a) Locomotor activity (average movements/min, mean ± SE) during six 30-minute periods and baseline levels of corticosterone at the conclusion of each 30 min period in white-crowned sparrows ($N = 6$, mean ± SE), held on an 18:6 h light:dark photoperiod: Mid-day; Q (quiescence); EF (2 h of migratory restlessness); LF (4 h of migratory restlessness); FE (end of migratory restlessness at onset of photophase); Morning (2 h of photophase). *Denotes a significant difference ($P < 0.05$) in locomotor activity from Mid-day, Quiescence and Morning samples. †Denotes a significant difference ($P < 0.05$) in baseline levels of corticosterone from the Morning sample (from Ramenofsky et al., 2008, courtesy of ©Medimond S.r.l.). (b) Compilation of results from independent studies illustrating mean ± SE locomotor activity and baseline corticosterone levels measured at mid-day (Mid) and during the quiescent (Q) phase in white-crowned sparrows held on an 18:6 h light:dark cycle and extending the scotophase by 8, 26 and 48 h (from Ramenofsky et al., 2008, courtesy of ©Medimond S.r.l.). (c) Mean corticosterone levels in white-crowned sparrows measured during migratory restlessness (baseline control levels) and during early migration (stress response) (redrawn from a compilation of several studies; Romero & Wingfield, 2016).

local nomadic movements to find refuge, settlement in an area conducive to breeding when available, establishment of a territory and attraction of a mate, followed by courtship, copulation and onset of nesting (Martin & Wiebe, 2004; Wingfield et al., 2004). All these events are dependent upon local conditions such as weather, predators and food. Although the reproductive system is ‘ready to go’, the onset of nesting does not occur automatically and does not commence until environmental conditions are favourable; that is, there appears to be a ‘brake’ to the onset of nesting, especially in females (Wingfield et al., 2016). This sequence of events is highly flexible and reversible because the Arctic spring is notoriously unpredictable and songbirds need to be highly mobile looking for patchy resources to survive until environmental conditions improve and become conducive to settlement and breeding. The problems associated with arrival and a short breeding season can be summarized as follows (Wingfield & Hunt, 2002).

1. Birds arrive in spring when conditions are still severe compared to wintering grounds.
2. Food supply early in the season is unpredictable in space, amount and type.
3. The breeding season in the Arctic is brief and individuals must initiate nesting as soon as possible despite severe conditions.
4. Even when nesting has begun, the birds must ‘resist’ the acute stressors of high predation risk and inclement weather throughout the breeding season, but none the less should abandon breeding and revert to local nomadic behaviour to find refuge and temporarily suspend territorial and reproductive behaviour when weather conditions become too severe to continue nesting.

Although migrant birds arrive at more or less the same time each year (Wingfield & Hunt, 2002; Wingfield et al., 2004), whether they can actually settle, and where, depends upon snow depth and patterns of snow melt (Hahn et al., 1995). Although in the brief Arctic spring we might expect rigid control mechanisms for gonadal growth and onset of breeding, there are nevertheless many examples of flexibility. Extensive data collected at a field site at Toolik Lake on the north slope of Alaska indicate that songbirds arrive with testes and ovaries in a near-functional state regardless of local conditions. Females are capable of initiating final maturation (yolk deposition in ovarian follicles) and laying eggs within days of arrival, but the actual dates that first eggs are laid may vary across years depending upon snow melt. For example, in 1991, snow melted out by the first week in May, but in 1992, deep snow cover and subfreezing temperatures persisted until the last week of May and into June. Although timing of gonadal development is more or less the same in each year, the actual location where birds settle and nest is dependent upon local conditions such as snow cover. These findings suggest that some Arctic birds may be spatially opportunistic (nomadic) especially at the limits of breeding range at high latitudes (Hahn et al., 1995).

HORMONAL BASES OF ARRIVAL BIOLOGY IN ARCTIC-BREEDING BIRDS

Environmental cues such as changing daylength (photoperiod) allow migrants to predict future events and time migration to arrive in mid-May. They also regulate reproductive function preparations for the breeding season (Dawson, King, Bentley, & Ball, 2001). In contrast, responses to local, unpredictable perturbations of the environment require rapid, facultative changes in behaviour and physiology. The latter have been collectively termed the emergency life history stage (ELHS), diverting the individual into a physiological and behavioural state that will promote survival (Romero & Wingfield, 2016; Wingfield et al., 2004). Although the ELHS is highly adaptive in most conditions, it may actually be detrimental in arriving Arctic birds because breeding must begin as soon as conditions allow and not be delayed unless weather is very severe. Rapid transitions among behavioural states of loose flocks on the move, including settlement and the onset of reproductive behaviours, involves aspects of ELHS, migration and breeding life history stages. Next we focus on the role the hypothalamo–pituitary–adrenal cortex (HPA) axis may play in orchestrating these complex transitions.

Vertebrates in general activate the HPA axis in response to environmental perturbations (Sapolsky et al., 2000). Adrenocorticotropin (ACTH) and endorphin are released from the precursor molecule pro-opiomelanocortin in the anterior pituitary under the control of corticotropin releasing factor (CRF) from the hypothalamus. ACTH acts primarily on the adrenocortical cells to promote synthesis and secretion of glucocorticoids (corticosterone in birds). Chronic elevation of corticosterone over weeks can have severe debilitating effects such as inhibition of the reproductive system, suppression of the immune system, promotion of severe protein loss from skeletal muscle, disruption of second cell messengers particularly the arachidonic acid cascade, neuronal cell malfunction and suppression of growth (Sapolsky et al., 2000). In birds and mammals, glucocorticoids also have several behavioural and physiological effects that promote fitness at least in the short term. These effects include suppression of reproductive behaviour without inhibiting the reproductive system, regulation of the immune system, increased gluconeogenesis, regulation of foraging behaviour, promotion of escape (irruptive) behaviour during the day and promotion of night restfulness and facilitation of recovery when the perturbation has passed (Romero & Wingfield, 2016; Sapolsky et al., 2000). These short-term effects suppress ‘unnecessary’ physiological and behavioural functions, activate alternate behavioural and physiological patterns that promote survival and avoid the long-term, detrimental effects of stress-induced high levels of corticosterone.

Do migrants arriving in the Arctic have to resist the potential for stress (Holberton & Wingfield, 2003) despite extreme conditions? Our initial working hypothesis was that, at arrival, adjustments of hormonal responses to stress allow individuals some degree of resistance until environmental conditions improve (Wingfield et al., 2004). More specifically, we predicted that a stress-induced increase in corticosterone levels, as measured by a standardized test of capture, handling and restraint, would be inhibited at arrival in the Arctic. This would provide resistance to the potential stress of severe weather with the benefit of enhanced reproductive success but at the potential cost of survival in the face of severe weather events. We found that the adrenocortical response to the standardized stress was greatly enhanced in males and enhanced to a lesser extent in females at arrival and up to the point of onset of nesting (Holberton & Wingfield, 2003; Wingfield & Ramenofsky, 2011). Given the established roles of corticosterone in both irruptive behaviour and nocturnal restfulness (reviewed in Romero & Wingfield, 2016; Wingfield & Ramenofsky, 1999), it is likely that corticosterone may play a preparative role for nomadic behaviour, with elevated plasma levels on arrival and settlement, followed by a decline of the adrenocortical response to stress after settlement on a territory and onset of nesting (Holberton & Wingfield, 2003; Wingfield et al., 2004; Wingfield & Ramenofsky, 2011). Furthermore, birds nesting at the leading edge of their existing range or after range expansion, where environmental conditions are likely to be most severe in spring, show the most extreme example of this modulation of the HPA response to perturbations (Krause et al., 2015; Walker et al., 2015).

Most, if not all, stressors have the potential to elicit increases in corticosterone secretion, although the time course and extent of the response may differ (Romero & Wingfield, 2016; Sapolsky et al., 2000). In Arctic birds that had already begun nesting and were incubating or feeding nestlings, a reduction in the adrenocortical response to stress was greater in the sex showing most parental care (Romero & Wingfield, 2016; Wingfield et al., 2004), and in the most severe environments. In contrast, prolonged severe weather (chronic stress) resulted in elevated adrenocortical responses to the standardized stress test and birds abandoned their nests and reformed flocks roaming the snow-covered tundra (Astheimer, Buttemer, & Wingfield, 1994). These studies suggest that in birds that are breeding, responsiveness to stress was initially suppressed, but can be reactivated. This indicates that flexibility in the intensity of the stress response is regulated, but the mechanisms are as yet unknown. Note that a nonmigratory subspecies of white-crowned sparrow (*Zonotrichia leucophrys nuttalli*) breeding in central coastal California did not show this type of modulation of the response to stress during breeding (Wingfield et al., 2004). Similar enhancement of the response to capture stress at the beginning of the nesting season has now been demonstrated in other sub-Arctic and Arctic avian populations compared to their lower-latitude congeners (e.g. bush warblers, *Cettia diphone*, in Hokkaido, Japan: Wingfield, Kubokawa, Ishida, Ishii, & Wada, 1995), snow buntings, *Plectrophenax nivalis*, and Lapland longspurs, *Calcarius lapponicus*, at the northern edge of their range at Thule, Greenland: Walker et al., 2015; white-crowned sparrows expanding northward in Alaska: Krause et al., 2015; red knots, *Calidris canutus*, in northern Canada: Reneerkens et al., 2002). In white-crowned sparrows, the increase in stress response was accompanied by decreased sensitivity to glucocorticoid feedback (Astheimer et al., 1994) and enhanced response of the adrenal cortex to ACTH (Romero, Ramenofsky, & Wingfield, 1997; Romero & Wingfield, 1999), allowing an overall increase in baseline as well as capture stress-induced plasma levels of corticosterone.

Note that circulating glucocorticoids are bound to corticosteroid-binding globulin (CBG), and while bound to this protein, it is believed that they cannot enter cells and interact with receptors that mediate biological actions (Malisch & Breuner, 2010). If this is the case, then it is possible that CBG levels are modulated to buffer increases in responsiveness to stress. Given the pronounced modulation of the adrenocortical responses to stress during arrival and settlement, we predicted that CBG levels would increase to buffer rapid and extensive changes in corticosterone secretion (Wingfield et al., 2004). The enhanced adrenocortical response to acute stress following arrival in the Arctic in male *Z. l. gambelii* was accompanied by an increase in CBG levels consistent with the buffer hypothesis (Breuner et al., 2003; Romero & Wingfield, 1999). In contrast, a non-Arctic-breeding subspecies of white-crowned sparrow (Puget Sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis*) did not increase responsiveness to stress in early spring and had a lower binding capacity of CBG, resulting in higher free levels of corticosterone 30 min postcapture than in *Z. l. gambelii* (Breuner et al., 2003). These results are consistent with our original hypothesis that the adrenocortical response to stress was reduced even though total levels of corticosterone (bound and unbound to CBG) were high. In other words, the free corticosterone levels at baseline and after acute stress can be buffered by high levels of CBG, ameliorating any immediate and potentially deleterious effects. Furthermore, there is evidence that the rise in CBG in early spring is regulated by rising testosterone levels in blood (Schoech, Ketterson, & Nolan, 1999), which would be appropriate as the onset of breeding draws near.

If the CBG buffer hypothesis is correct, then during severe weather events in spring, which trigger rapid nomadic survival behaviour, CBG levels in blood should be regulated down, thus releasing bound corticosterone (Malisch & Breuner, 2010). There is evidence that CBG binding capacity (a measure of how much CBG is present) can be regulated within hours if a stressor persists. In captive male *Z. l. gambelii*, 2 h of food restriction (to mimic the effects of a storm that covers food resources) increased plasma corticosterone levels but had no immediate effect on CBG binding capacity. After 22 h of food restriction, corticosterone levels were similar to controls, but CBG levels had declined and free corticosterone titres were higher (Lynn, Breuner, & Wingfield, 2003).

Thus far the evidence suggests that corticosterone–behaviour systems associated with arrival biology in Arctic birds are highly flexible, allowing high adrenocortical responses to stress at this time, but buffering the early effects with high CBG binding capacity. Although much more work needs to be done to assess how quickly changes in CBG binding capacity occur and how they change through the rest of the Arctic summer, this may be an intriguing system by which migrant birds arriving in the Arctic maintain high activity of the HPA axis but modulate the expression of the CBG gene and thus access of hormone to receptors. Other components of the HPA axis and target cells may also be regulated, particularly corticosterone receptors.

In mammals and birds there are two intracellular genomic receptors for corticosterone. Once bound to corticosterone, the receptor–hormone complex becomes a gene transcription factor regulating a broad spectrum of genes associated with the stress response and survival (e.g. Breuner et al., 2003; Sapolsky et al., 2000). These actions usually take hours for protein synthesis to be effective and therefore represent longer-term responses. One receptor type is the mineralocorticoid receptor, which has a high affinity for corticosterone and can bind (i.e. be activated) at baseline levels. A second receptor type is the glucocorticoid receptor, which has a low affinity for corticosterone and binds at higher ‘stress’ levels (Breuner et al., 2003). In vitro binding experiments show that the mineralocorticoid receptor-like receptor in white-crowned sparrows has high affinity for corticosterone but has different specificity characteristics from the mammalian counterpart (Breuner et al., 2003). The glucocorticoid-like receptor has a lower binding affinity for corticosterone similar in specificity to that of mammals (Breuner et al., 2003) and is only activated at higher circulating concentrations of corticosterone. There were no significant differences in binding capacity of glucocorticoid receptors in the liver or the brain of *Z. l. gambelii* (Arctic-breeding) and *Z. l. pugetensis* (mid-latitude-breeding) males. Using mean levels of free corticosterone and glucocorticoid receptor capacity, it is possible to calculate the receptor occupancy (hormone bound) during stress. Although binding capacity of glucocorticoid receptors did not vary between the two subspecies of white-crowned sparrow, more glucocorticoid receptors were occupied by corticosterone at 30 min postcapture in both the liver and the brain of *Z. l. pugetensis* (Breuner et al., 2003). These studies strengthen the argument that CBG buffering actually decreases sensitivity to stress in *Z. l. gambelii* arriving in the Arctic.

There is also a nongenomic membrane receptor mediating more rapid (within minutes) effects of corticosteroids (Breuner, Greenberg, & Wingfield, 1998). When plasma levels of corticosterone in male *Z. l. gambelii* were increased rapidly, but noninvasively (i.e. by feeding them mealworms injected with known doses of corticosterone), an equally rapid increase in perch-hopping activity occurred within 10 min compared to controls. This rapid action is inconsistent with genomic receptor action, which requires at least 30 min and usually several hours (Breuner et al., 1998; Breuner & Wingfield, 2000). Interestingly, a lower dose of corticosterone, consistent with intermediate plasma levels, was most effective in increasing locomotor activity. A higher dose, inconsistent with high stress levels, had no effect on activity (Breuner et al., 1998; Breuner & Wingfield, 2000). Furthermore, actions of this putative membrane-type receptor appear to be greatest in spring (upon arrival to the Arctic breeding ground) and less so in winter (Breuner & Wingfield, 2000). These studies suggest that rapid effects of corticosterone on activity may be related to final stages of spring migration in the Arctic when birds arrive on their breeding grounds, and are important in the regulation of locomotor activity associated with locating suitable breeding habitat and familiarizing themselves with local food sources should conditions deteriorate.

Stress levels of corticosterone (as generated experimentally by subcutaneous implants of corticosterone) were predicted to elevate locomotor activity in male *Z. l. gambelii*, but the high levels of corticosterone actually reduced activity during the day (Astheimer, Buttemer, & Wingfield, 1992). However, when corticosterone-implanted white-crowned sparrows were deprived of food, they showed an increase in perch-hopping activity as well as escape type behaviour (Astheimer et al., 1992). This activity differs from that observed by Breuner et al. (1998) and suggests two distinct effects of corticosterone on activity (Romero & Wingfield, 2016). A question that arises from these studies is how one steroid hormone, corticosterone, can have effects on different types of activity and in different contexts (presence/absence of food). It is possible that corticosterone has permissive and preparative roles and the final behaviour shown depends on synergistic actions with other hormones or with central secretions that more directly affect behaviour. Additional experiments indicate that irruptive type behaviour (and its perch-hopping equivalent) is also influenced by the brain peptide corticotropin-releasing factor (CRF) injected centrally into the third ventricle of male *Z. l. gambelii* in the laboratory (Maney & Wingfield, 1998), as well as by central injections of CRF into the lateral ventricles of male *Z. l. gambelii* in the field (Romero, Dean, & Wingfield, 1998). Thus, corticosterone action may play a permissive role for secretion of brain peptides, or other substances, that may provide specificity of behaviour for particular environmental scenarios as well as some behavioural flexibility needed to respond to unpredictable weather events by switching back from territorial behaviour to flocking and searching for refugia.

Another complex transition from arrival biology to breeding is the flexible interrelationships of flocking behaviour during severe weather and territorial behaviour and pair bonding as settlement occurs prior to nesting (Wingfield et al., 2004). It is well known that the gonads are near full maturation at arrival on the breeding grounds and that plasma levels of testosterone in males can be high at this time (Wingfield et al., 2004). However, the rapid switch from social to territorial and pairing behaviour may be more related to actions of brain peptides such as mesotocin and vasotocin (Goodson, Kelly, & Kingsbury, 2012; Goodson, Wilson, Schrock, 2012). Although we have little information for Arctic-breeding songbirds, in other species from lower latitudes, central actions of mesotocin may accompany pair bonding and vasotocin may be involved in aggression associated with territoriality (Goodson & Evans, 2004; Goodson, Kelly et al., 2012; Goodson, Wilson et al., 2012). In free-living male *Z. l. gambelii*, central injections of vasotocin into the third ventricle had no effect on their responses to a simulated territorial challenge compared to controls given saline (Romero et al., 1998). However, central injection of CRF did significantly reduce male responses to simulated territorial intrusions (Romero et al., 1998). The roles of these brain peptides may be pivotal for the transition from migration to breeding in Arctic birds but more data are needed.

TRANSITIONS TO BREEDING: POTENTIAL ROLE OF A NOVEL PEPTIDE

As birds arrive in the Arctic, settle and transition to the onset of nesting, reproductive hormones become critical for final maturation. In female white-crowned sparrows this involves increases in luteinizing hormone and oestradiol that culminate in final maturation of ovarian follicles leading to ovulation (Wingfield & Farner, 1993). In males, luteinizing hormone and testosterone are elevated as females become sexually receptive (Wingfield & Farner, 1993). Photoperiodic regulation of reproductive development in spring involves secretion of chicken gonadotropin-releasing hormone I (cGnRH-I), a major GnRH in passerines (Bentley, Perfito, Ukena, Tsutsui, & Wingfield, 2003). Although studies of the different forms of GnRH and its receptors have revealed a wealth of information as to their function, a directly inhibitory neuropeptide for gonadotropin release has, until recently, remained unknown. A neuropeptide that specifically inhibits avian pituitary gonadotropin release in vitro, gonadotropin-inhibitory hormone (GnIH), was discovered over 15 years ago (Tsutsui et al., 2000). The gonadotropin inhibitory system is an intriguing concept and provides us with an unprecedented opportunity to study the regulation of reproduction from an entirely novel standpoint. This is critical for Arctic-breeding songbirds because when the onset of nesting occurs, sudden snow storms halt final maturation of the ovary, and birds abandon territories and form wide-ranging flocks (Wingfield et al., 2004). How is this flexibility of switching from nomadism to settlement and breeding regulated while keeping the reproductive system in a near functional state? GnIH is a candidate for regulating the reproductive side of these transitions (as reviewed in Wingfield et al., 2016).

The GnIH gene has been cloned in the brain of *Z. l. gambelii* (Osugi et al., 2004), and it was demonstrated that only neurons of the paraventricular nucleus (PVN) in the hypothalamus express this gene. However, fibres emanating from these neurons project to multiple brain locations, including the median eminence and brainstem (Bentley et al., 2003). Such distribution suggests multiple functions within the central nervous system. In vivo experiments show that, in white-crowned sparrows, GnIH rapidly and consistently (within 2 min) attenuated the GnRH-induced rise in plasma luteinizing hormone (Osugi et al., 2004). The mechanism(s) controlling GnIH production and release are unknown at present. Potentially, combinations of GnRH and GnIH levels may regulate release of pituitary luteinizing hormone and follicle-stimulating hormone, which in turn orchestrate gonadal growth and secretion of sex steroid hormones. Furthermore, temporary gene silencing of GnIH in brain of photostimulated *Z. l. gambelii* results in increases in singing and reproductive behaviours that accompany the onset of nesting (Ubuka et al., 2012). The role of GnIH associated with arrival in the Arctic, expression of reproductive behaviour, onset of breeding and its termination is particularly pertinent given the high degree of behavioural and physiological flexibility required to cope with such a severe environment (Wingfield, 2015; Wingfield et al., 2016). Growing evidence also suggests a positive interrelationship of GnIH and environmental stress (Calisi, Rizzo, & Bentley, 2008) that will likely shed new insight on arrival biology in the Arctic. Interrelationships of GnIH neurons and stress-induced increases in glucocorticoids deserve further investigation.

Conclusions

A concept of how migrant songbirds use the Arctic landscape is emerging not only on arrival but also during breeding and when forced to abandon territories and wander because of severe weather events. We have the basis of a framework outlining how a highly flexible control system orchestrates complex transitions and reversals of behaviour and physiology in response to a highly unpredictable environment. Future investigations will further probe the mechanisms underlying these complex transitions in breeding behaviour and physiology. As global climate change progresses, many species will be shifting their geographical range for breeding, and with the increase in frequency, intensity and duration of weather events, it is likely that transitions of life history stages will become more unpredictable and will need to be very flexible. The arrival biology of Arctic birds may be a useful model providing insight into how these complex transitions may be regulated in a broader sense.

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