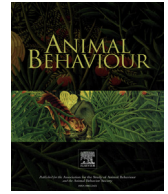




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Regulation of complex behavioural transitions: migration to breeding

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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.

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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 sub-stages 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, & Ramenofsky, 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 (Falson, 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

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