



## Arctic spring: the arrival biology of migrant birds \*

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**Abstract** On arrival in the Arctic, migrant birds must adjust their physiology and behavior to unpredictable snow cover, weather, food sources and predator pressure. In other words they must be resistant to environmental perturbations (stress) so that they can migrate to their tundra nesting areas and settle on territories as soon as possible. They can then begin breeding as soon as when environmental conditions become favorable. They do this partly by using micro-habitats such as areas where snow depth is low, and patches of tundra that melt out rapidly (especially near willows *Salix* sp). Ground temperatures increase dramatically within hours after exposure to sun; and invertebrate activity begins simultaneously. Wind speeds are attenuated almost completely within 10 cm of the ground in willows and tussock tundra. The combination of these conditions provides an ideal refuge, especially for passerine migrants in early spring. However, if conditions worsen, the birds can leave. There are adjustments of the adrenocortical responses to stress because arctic conditions in spring are potentially severe, at least compared with wintering grounds to the south. Secretion of corticosterone in response to acute stress is enhanced at arrival in males, accompanied by a decrease in sensitivity to negative feedback and a change in responsiveness of the adrenal cortex cells to adrenocorticotropin. There is also an increase in levels of corticosterone-binding globulin (CBG) so that the actions of corticosterone are buffered according to the severity of environmental conditions. Regulation at the level of genomic receptors, particularly the low affinity glucocorticosteroid-like receptor for corticosterone in brain and liver, may be important; and non-genomic actions of corticosterone may play a major role too. In other words, the hormone-behavior system associated with arrival biology is highly flexible [*Acta Zoologica Sinica* 50 (6): 948–960, 2004].

**Key words** Arctic, Migration, Stress, Adrenal, Corticosterone, Receptor

## 北极的春季：迁徙鸟类抵达的生物学 \*

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**摘要** 一旦鸟类抵达北极区, 迁徙鸟类必须调整其生理和行为以适应不可预知的雪盖、天气、食物资源和天敌胁迫。换言之, 他们必须抵抗环境干扰(压力)以便尽早迁徙到苔原上的巢区并建立领域。然后, 一旦外界环境有利时, 它们就立即开始繁殖。这些鸟类的繁殖有一部分是利用低雪盖区域的微生境以及雪融较快的苔原斑块(特别是在柳树 *Salix* sp. 附近)。在北极地区, 地面温度在日照若干小时后急剧上升, 同时无脊椎动物开始活动。风速在地面柳枝和生草丛苔原 10 cm 下几乎减弱为零。这些条件结合在一起提供了理想的避难所, 对于早春迁徙到此的雀形目鸟类尤其如此。然而, 如果环境调节变得更为恶劣, 这些鸟类会离开。因为与南方越冬地相比, 春季北极区条件具有潜在的严酷性, 所以鸟类对于应激时的肾上腺皮质反应有所调整。雄鸟到达北极地区时对于剧烈应激刺激下的肾上腺酮的分泌有所提高, 并且伴随着对于负反馈敏感性的下降和肾上腺皮质层细胞对于促肾上腺皮质激素作用反应的变化。同时, 肾上腺酮结合蛋白(CBG)的水平也有所提高, 以至于肾上腺酮的作用在恶劣的环境条件下得到缓冲。基因组受体水平的调节, 尤其是在脑和肝脏中糖皮质激素类固醇类似受体与肾上腺酮的低亲和力, 以及肾上腺酮的非基因组水平的作用, 可能是很重要的。换言之, 与抵达生物学有关的激素-行为系统是高度可变的[动物学报 50(6): 948-960, 2004]。

**关键词** 北极 迁徙 应激 肾上腺 肾上腺酮 感受器

## 1 Introduction

The vagaries of arctic weather in spring have been appreciated by indigenous peoples for millennia. For example, an old Finnish proverb states, “The northern summer is short and variable”. Another proverb from the Saami Reindeer People asserts that “(arctic) spring is the weather’s struggle-time” (Järvinen, 1989). That phrase describes spring in the Arctic perfectly. Weather swings dramatically between winter-like conditions with high winds, low temperatures and snow to sudden breaks in the weather with sunshine and rapidly increasing temperatures. Spring on the North Slope Borough of Alaska is notoriously unpredictable. Temperatures early in spring are more unpredictable than those later in summer (Myers and Pitelka, 1979). At our field site near Toolik Lake (67°N), snow may melt from the tundra as early as the first week in May, but subsequent storms (and temperatures down to  $-11\text{ }^{\circ}\text{C}$  or lower) may inundate early migrants. In some years, snow and sub-freezing temperatures may persist into late May (Hahn et al., 1995). In the higher Arctic, weather is even more severe.

Virtually all avian species that breed on the arctic tundra are migratory, spending the winter in temperate and tropical latitudes (Piersma, 1994; Pielou, 1994). As a result, arctic weather in spring may present a considerable challenge. On their return in spring, arctic migrants face two major environmental constraints associated with arrival. First, they must establish a breeding territory, attract a mate, and begin nesting on the tundra breeding grounds as early as feasible (O’Reilly and Wingfield, 1995). The ephemeral arctic summer is so brief that birds arriving late may fail to reproduce. Secondly, early arrival in the Arctic is fraught with problems due to capricious

weather. Therefore, birds must also adjust their physiology and behavior to withstand severe weather and sudden food shortages (O’Reilly and Wingfield, 1995). Collectively, these events and the adaptations to deal with them, can be called “arrival biology”. These phenomena have been less well investigated than the “stop-over” biology of migrating birds (Berthold, 1996), but nonetheless may be critical for the transition between vernal migration and onset of breeding.

In this overview we will consider the problems that migrants face, how they move into arctic habitats when conditions are severe, and how they then establish territories in the face of potentially stressful conditions. What are the environmental conditions like in the microhabitats that migrant birds utilize as they move out on to the tundra? These issues are critical if breeding is to begin as soon as possible when the arctic summer begins. Then we will address possible hormone-behavior adaptations and resistance to the potential stress of an arctic spring. Exposure to severe weather in the arctic spring has the potential to induce hormonal responses to stress that in turn have well-known inhibitory effects on reproductive function (e.g., Moore and Miller, 1984; Greenberg and Wingfield, 1987). For example, on May 16 and 17, 2001, night air temperature at Toolik Field Station dropped to  $-20\text{ }^{\circ}\text{C}$  and did not rise above freezing during the day. Furthermore, blizzards and sub-freezing temperatures can occur unpredictably at any time during the summer, posing further problems for both adults and their young (Astheimer et al., 1992).

Hormone-behavior interactions that allow territory establishment and pair formation to occur in the face of potentially extreme conditions would be adaptive, given that conditions in the immediate future are

likely to be conducive to raising young. Although the physiological ecology of arctic animals in relation to cold has received considerable attention (e.g., Barnes and Deviche, 1995), adaptations of reproductive behavior, their interrelationships with hormones and resistance to environmental stress are just beginning to be explored. Indeed, migrant birds in the Arctic do not have time to be distracted by stress. Do they then modify the adrenocortical hormone response to stress? That is, do they become more resistant? This may be costly in terms of energy, but the benefit is reproductive success.

## 2 Arrival biology of migrant birds

Arrival dates of migrant birds at Toolik Lake, Alaska, are precise: May 17 – 22 for both passerines and charadriiforms. Occasionally some individuals may arrive earlier and many arrive much later, but the main influx of migrant birds is generally within these dates. Although the arrival dates of many migrants are consistent from year to year, arctic weather and snow cover can vary dramatically. Snow cover can be complete at arrival time in one year, and very patchy in another (Fig.1). Additionally, year-to-



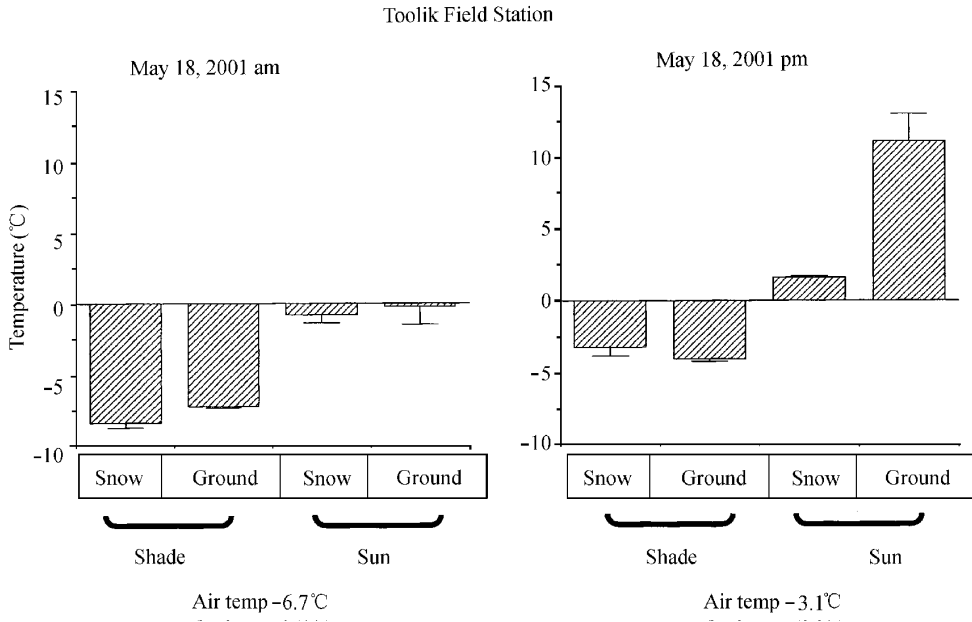
year snow cover along the migratory route may have no bearing on concurrent conditions on the breeding grounds further north (Fig.1). In 2002, snow cover to the south of the Brooks Range in Alaska was complete and very deep at the time passerine migrants were passing through; yet just to the north of Atigun Pass, snow had completely melted. Clearly, migrant birds cannot predict snow cover and depth on the breeding grounds until they arrive. Even after arrival, snow storms with high winds can occur at any time, emphasizing the need for birds to seek out micro-habitats that allow them to shelter from such severe conditions.

### 2.1 Tundra micro-habitats as refuges for migrant passerines

By the third week in May, day length is virtually 24 hours and clearing skies may result in sunshine throughout most of the time. Direct sunlight can penetrate snow at depths up to 20 – 30 cm (depending upon density) and melt the snow pack from the ground up as well as the top down. Thus, depth of snow cover is important in determining which areas tundra will open up first and thus where many migrant birds will settle (Hahn et al., 1995). Wind

**Fig.1 Variation in arctic snow cover among years, and among localities within years**

The top two panels show how the same area near the Sagavanirktok River, approximately 25 km northeast of Toolik Field Station, North Slope Borough, Alaska, may have different snow cover in different years. The bottom two panels show snow cover north and south of Atigun Pass in the Brooks Range of Alaska. The Dalton Highway crosses the range through that Pass, which is used by large numbers of migrant passerines. It is about 50 km south of Toolik Field Station. Note that on May 17, 2002, snow cover to the south was deep and virtually 100% whereas to the north the tundra was completely exposed.



**Fig. 2** Temperatures recorded at the surface of snow cover and on melted-out tundra in sun and shade

Temperature probes were placed 1 cm below surfaces to avoid effects of direct sunlight. Temperature recordings were made at 20 locations in snow and on the ground in sun and shade. Cross-hatched bars represent means  $\pm$  standard errors. Air temperatures were recorded at each site, in shade at 1 meter above the surface of snow or ground.

action may scour ridges and some valleys reducing snow cover to a few centimeters. These areas typically melt out very quickly, often within hours. On May 17, 2001, morning snow cover in the Atigun Valley south of Toolik Field Station was over 80%. The day was sunny but windy with air temperatures ranging from  $-20^{\circ}\text{C}$  to  $-3^{\circ}\text{C}$ . Nonetheless, solar energy heated the ground sufficiently to reduce snow cover to about 10% of the valley floor by afternoon. The darker surface of the tundra absorbs radiant energy from the sun, resulting in higher temperatures at ground level compared with open-air temperature, an effect greatly enhanced in sunlight (Fig. 2). Temperatures at ground level in the sun, or just below it in leaf litter at approximately 1 cm depth, can be astonishingly high (Fig. 3).

But whenever incident radiation is reduced by cloud, physical barriers (i. e., sun passing behind a mountain), or a low sun angle (e. g., late in the day), temperatures plummet, often to below freezing (Fig. 3). Thus daily cycles of temperature at ground level can fluctuate widely and variably. Patches of tundra can become snow-free extremely rapidly to provide microhabitat for migrant birds. Furthermore, when late spring snow storms occur, the accumulation of snow on these bare patches is much lower than on existing snow pack, suggesting that once microhabitats open up, they can persist even during late snow storms (Hahn et al., 1995).

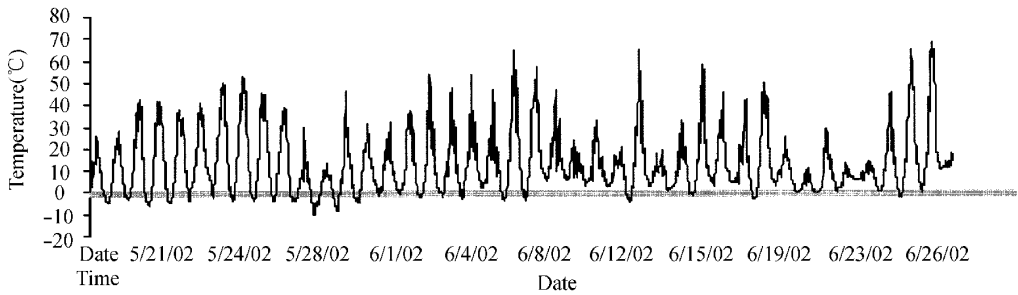
## 2.2 Food sources for migrant birds in the Arctic

Complete snow cover in spring can cover virtual-

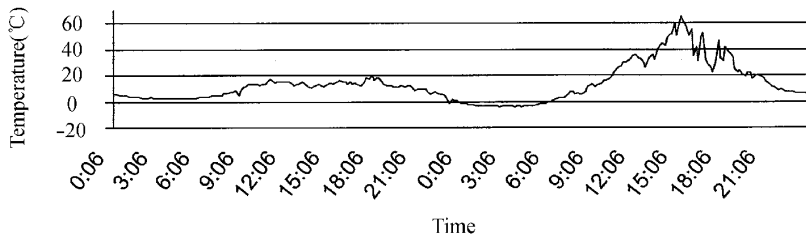
ly all food sources for migrating birds. Both the rock ptarmigan *Lagopus mutus* and willow ptarmigan *L. lagopus* can survive by eating only the tips of willow branches and their buds protruding from snow. Passerines such as snow buntings *Plectrophenax nivalis*, lapland longspurs *Calcarius lapponicus*, and redpolls *Carduelis flammea* can feed on seeds on exposed patches of tundra scoured free of snow by winds. However, they are also exposed to wind chill and possible predation. As soon as tundra patches melt out, increases in ground temperature and wind attenuation allow birds to forage in more benign conditions even though these areas are patchy and unpredictable both spatially and temporally. Such patches always offer seeds from herbs, grasses and shrubs. In some years, masting of the dwarf birch (*Betula* sp.) can result in a super abundance of seeds although this, again, is highly variable both spatially and temporally. As soon as patches of tundra melt out, berries (especially from *Vaccinium* sp.) from the previous summer become uncovered and are eaten in large quantities by migrant passerines. High ground temperatures in melted out areas also result in rapid emergence of arthropods (Insecta and Arachnida). We have observed live dipteran flies, beetles and wolf spiders up to 2 cm long within 2 hours of a patch of tundra becoming snow free. These arthropods are an important source of food for migrant birds.

As the first patches of tundra melt—usually on higher ground where snow depth is less because of wind action—water runs down under the snow pack

Atigun Ground Temps: North Slope, AK



Atigun Ground Temp: 48 hours



### 2.3 Temperature records using HOBO data loggers at a site in the Atigun Valley about 25 km south of Toolik Field Station during periods of 24 hours of daylight in late May and June

Note that throughout spring into summer there are dramatic fluctuations in ground temperatures. Probes were placed 1 cm beneath leaf litter and other surface vegetation to avoid direct sun light. Temperatures may approach 50°C on sunny days but fall close to freezing on cloudy days. Note also that during the day, ground temperature may vary dramatically according to the angle of sunlight and also if the sun passes behind a mountain ridge, thus shading the ground (lower panel).

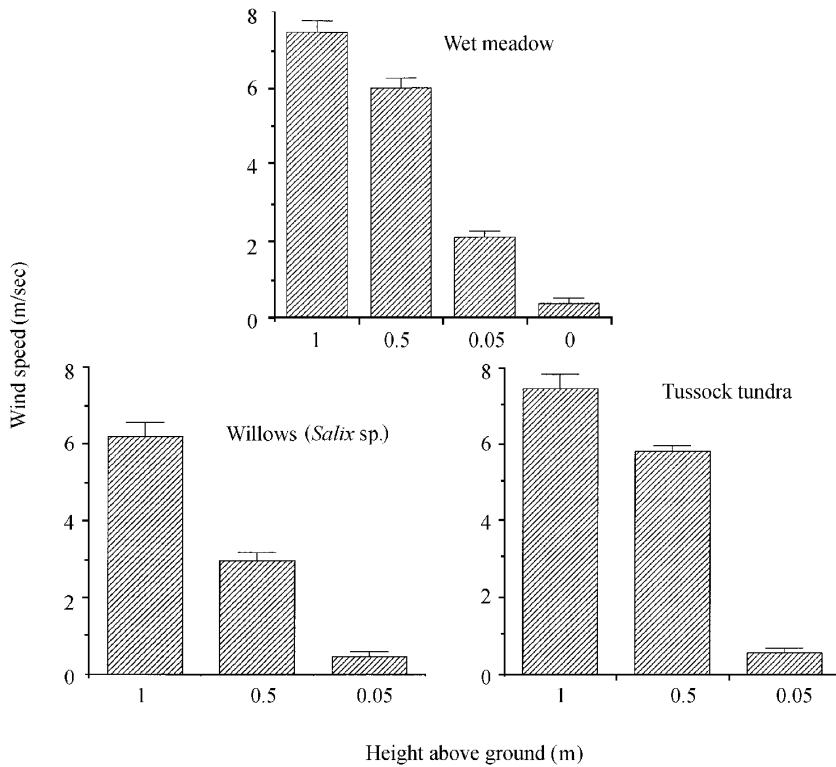
to emerge in valleys or shallow depressions. This water may form ephemeral streams and ponds in deeper snow. We have observed migrant passerines and shorebirds (Scolopacidae) feeding along the edge of these streams and ponds in snow. Closer inspection revealed that the flow of water under the snow had washed out seeds and arthropods from the surface of the tundra beneath, concentrating them along the edge of the water where the migrant birds had access. These areas are conspicuous because emerging water discolors the snow. Additionally, winter winds form drifts that also act as traps for wind-blown seeds. As the snow melts, water percolating down concentrates seeds usually at the lower edge of the drift; these are thus rich feeding areas for granivorous birds. Additional detritus (dead vegetation and dust) discolors the snow, making such patches conspicuous.

Therefore within hours a frozen, snow covered, landscape can become scattered with patches of open tundra that provide temperatures higher than the surrounding air, shelter from high winds, and multiple sources of food. These resources, however, are still vulnerable to the unpredictable storms that can occur at any time, covering snow-free refuges and refreez-

ing water to lock in washed out food items.

### 2.3 Wind attenuation in micro-habitats

One of the most severe climatic problems for migrant birds on the tundra is high wind speed. This coupled with low temperature can result in extreme wind chill factors. Furthermore, access to foraging patches, and movement between them, can quickly become more restricted; thus competition for food may become a concern in addition to body temperature regulation. Nevertheless, wind speed can be greatly attenuated close to the ground, especially as patches of tundra open up with local snow melt (Fig.4). Even on exposed grassy meadows wind speed is attenuated by about 75% within 5 cm of the ground. In willow patches and tussock tundra, wind speeds may be reduced by over 90% (Fig.4). Thus, the patches of tundra that melt out first are not only much warmer than air temperatures, but they also provide shelter from wind, thereby greatly reducing wind chill. Migrating birds may only be exposed to truly severe conditions when they move from one patch to another over snow-covered areas. However, sudden onset of inclement weather, particularly snow storms, may force them into ever shrinking patches of



**Fig. 4** Wind speed attenuation from 1 meter above the ground down to 5 cm in different tundra habitats

Cross-hatched bars are means with standard errors ( $n =$  at least 20). Wind speeds were measured with a handheld anemometer.

micro-habitat. This in turn will increase the density of birds in a patch, resulting in competition for food.

#### 2.4 Habitat use by arriving migrants

Observations of migrating passerines arriving near their breeding grounds indicate that they use the micro-habitats formed by melting snow. On May 16, 2001, no passerines were to be seen north of the Toolik Field Station, and snow cover was essentially 100%. On May 17, a single horned lark *Eremophila alpestris* and two male lapland longspurs flew by the field station and then disappeared. Further south, toward the Brooks Range, patches of snow began to melt out and passerines were observed moving north from patch to patch (Table 1). At Atigun Pass (1 250 m a. s. l.) snow cover was 100%, but lapland longspurs and American tree sparrows *Spizella arborea*, were flying north through the pass. To the south in the Chandalar Valley, snow cover was much less and water was flowing. Here, flocks of American tree sparrows, American robins *Turdus migratorius*, and Gambel's white-crowned sparrows *Zonotrichia leucophrys gambelii*, were moving north. As the day progressed, flocks of 20 or more lapland longspurs, American tree sparrows and Gambel's white-crowned sparrows crossed the Brooks Range summit near Atigun Pass and descended to the Atigun Valley. One patch of willows (*Salix* sp.) on the north side of Atigun Pass provided the first refuge for passerines crossing the Pass. Passerines were con-

stantly observed flying down from the snow covered pass, and out of a side valley, into the willows. Later in the day, weather conditions deteriorated and over 200 lapland longspurs were observed flying back south toward Atigun Pass. From this first refuge it is only 5–8 km to the south side of the pass and the Chandalar valley where conditions were much milder with water flowing. These observations indicate that migrating passerines moving north of the Brooks Range can also return south to more benign conditions over a relatively short distance.

In 2002, conditions at arrival were very different (Fig. 1). On May 16, snow cover was less than 25% at Toolik Field Station and water was flowing. Except for 6 redpolls north of the field station, there were no passerines. On the morning of May 17, lapland longspurs began arriving in flocks of 2–25; and American tree sparrows and horned larks also appeared further south in the Atigun Valley. South of the Pass, in the Chandalar Valley, snow cover was 100% (Fig. 1) and no water was flowing. It was the reverse, climatically, of 2001; but nevertheless, passerines were moving north along the Dalton Highway, the only snow free area by the road. Gambel's white-crowned sparrows were present in the Chandalar Valley but did not appear in the Atigun Valley north of the pass until May 18. Thus, although the first arrivals appeared on the same two days in two years, conditions facing them as they moved north

were very different. Note that in 2002, passerines were generally only found where snow free areas exposed micro-habitats (Table 1).

**Table 1 Observations of arriving migrant birds north of the brooks range in relation to snow cover**

Species	Snow	Melt-out Area	Total
Lapland longspur	1	17	18
<i>Calcarius lapponicus</i>			
American tree sparrow	1	13	14
<i>Spizella arborea</i>			
White-crowned sparrow	0	14	14
<i>Zonotrichia leucophrys gambelii</i>			

Numbers of observations of birds in snow-covered areas with no bare ground versus melted-out areas with bare ground, willows (*Salix* sp.), dwarf birch (*Betula* sp.) and tussock tundra. All observations were made when birds were first arriving on May 17 and 18, 2001 and 2002. Right hand column is the total number of observations made. At each observation, snow-covered areas and melt out areas were surveyed. These three species of migrating passerines clearly favored melt-out areas to complete snow cover.

## 2.5 Predators of migrant birds in the Arctic

There is considerable evidence that populations of predators at northern latitudes can fluctuate dramatically (Newton, 1998). In 2001, at our study site at Toolik Lake, numbers of microtine rodents were very high as were their primary predators: red foxes *Vulpes vulpes*, rough-legged hawks *Buteo lagopus*, short-eared owls *Asio flammeus*, and northern harriers *Circus cyaneus*. As migrant birds began moving on to the tundra, a storm blew in that deposited at least 10 cm of new snow. As a result, the avian predators of voles could presumably no longer locate the rodents and began attacking the flocks of migrant passerines. Additionally, snow cover reduced the number of patches of snow-free micro-habitat, resulting in increased density of migrant birds. Many species formed flocks feeding not only in micro-habitat, but also over snow-covered areas where the seed heads of grasses protruded above the surface. For the next two days, migrants were harassed repeatedly by avian predators that normally did not prey upon them.

Further evidence indicates that predator pressure varies dramatically both within and among years (Newton, 1998). After arrival, nest predation of lapland longspurs fluctuated from year to year (Wingfield and Hunt, 2002). In northern Scandinavia, red fox numbers fluctuated synchronically with vole (*Microtus* sp.) cycles, and foxes switched to ground-nesting birds when voles were scarce. Fox numbers, and their propensity to focus on birds as prey, can thus be unpredictable (Lindstrom et al., 1994). In the islands of northern Sweden, grouse numbers correlated with vole abundance, i. e., predators turned more to grouse when voles were sparse. Removal of predators (red foxes and martens *Martes martes*)

was followed by increased reproductive success in the capercaillie *Tetrao urogallus*, and black grouse *T. tetrix* (Marström et al., 1988). Clearly, predation can have a major influence on survival during the arrival period, as well as on reproductive success. Moreover, Silverin (1998) showed in the pied flycatcher *Ficedula hypoleuca* that the presence of certain types of nest predator resulted in an increase in corticosterone levels in adults. In the Arctic, the breeding season is so short that birds cannot delay nesting; and if they lose a nest to a predator, re-nesting is rare. Arctic breeding birds simply cannot wait for predator pressure to abate before initiating breeding, unlike the situation in the tropics where the presence of predators may actually be an ultimate factor in regulating the timing of breeding (Morton, 1971).

## 2.6 Arrival biology: problems facing migrant birds in the Arctic

Although changing day length as spring progresses is a reliable predictor of the short breeding season, migrant birds arriving on the tundra face a number of unpredictable phenomena. They must be flexible to adjust to variable snow cover, and be prepared to respond to further storms. Patchy snow-melt reveals micro-habitats that provide higher temperatures and reduced wind chill while at the same time uncovering variable food resources. However, these habitats can become inaccessible if a severe storm inundates them with snow. Additionally, numbers and types of predators may vary from year to year in an unpredictable manner. These unpredictable characteristics of the Arctic environment require behavioral and physiological plasticity. For example, migrants must be prepared to retreat during storms, at least to the nearest refuge, usually but not always to the south. Responses to these potentially stressful events must achieve a balance between threats posed to survival from physical stress under severe conditions and the risk of missing a single reproductive opportunity. Mechanisms must be in place for responding, or not responding, to potential environmental stressors. Furthermore, these mechanisms must be fine-tuned to a particularly capricious environment. The endocrine mechanisms permitting migrant birds to survive as they arrive on their breeding areas will be considered next.

## 3 Possible hormonal bases of arrival biology

Arrival on the tundra poses many problems associated with potential stress. Weather is only one source of unpredictable events (labile perturbation factors, LPFs). Other examples include sudden changes in social status (territoriality to flocking as patches of micro-habitat shrink during storms), in-

creased predator numbers, and decreased food resources (Wingfield et al., 1998; Wingfield and Ramenofsky, 1999; Wingfield and Romero, 2000). Environmental cues such as changing day length allow migrants to predict future events and to time migration to arrive in the third week of May. However, responses to LPFs require more rapid facultative changes in behavior and physiology than follow those from anticipation. These responses have been collectively termed the emergency life history stage (ELHS) that diverts the individual into a physiological and behavioral state that will allow survival in the best condition possible (Wingfield et al., 1998). Although the ELHS is highly adaptive in most conditions, it may actually be detrimental in migrants arriving on the tundra because the birds must settle on breeding territories as soon as possible so that breeding can begin as soon as local conditions allow. Thus it was hypothesized that, during arrival, there may be adjustment of hormonal responses to stress that allow individuals some degree of "stress-resistance" until environmental conditions improve (Wingfield, 1994).

Vertebrates activate the hypothalamo-pituitary adrenal (HPA) axis in response to LPFs (Greenberg and Wingfield, 1987). Adrenocorticotropin (ACTH) is released from the precursor molecule pro-opiomelanocortin in the anterior pituitary under the control of corticotropin-releasing hormone (CRH) from the hypothalamus. ACTH acts primarily on the adrenocortical cells to promote synthesis and secretion of glucocorticosteroids. In birds, the primary glucocorticosteroid is corticosterone. 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 death and suppression of growth (e.g., Sapolsky et al., 2000). These effects would be clearly detrimental to an individual at any time. However, effects of transitory increases in corticosterone in response to LPFs are more adaptive. In birds and mammals, corticosterone has several behavioral and physiological effects that promote fitness, at least in the short term. These include suppression of reproductive behavior without inhibiting the reproductive system, regulation of the immune system, increased gluconeogenesis, regulation of foraging behavior, promotion of escape (irruptive) behavior by day, promotion of night restfulness, and facilitation of recovery on return to normal life history stage (Sapolsky et al., 2000; Wingfield and Romero, 2000).

These short-term effects of corticosterone during

responses to LPFs suppress "unnecessary" physiological and behavioral functions, activate alternate behavioral and physiological patterns that promote survival (i.e., temporary emergency behavior) and avoid the long-term, detrimental effects of stress-induced high levels of corticosterone. But, on spring arrival in the Arctic, migrants have to resist the potential for stress when exposed to many LPFs. Our hypothesis is that the adrenocortical response to LPFs is modulated, at least in the short term, to allow migrants to continue to arrive in the face of severe conditions. More specifically, we predict that the stress-induced increase in corticosterone levels would be inhibited at arrival, thus providing resistance to potential stress from severe weather. This may be energetically expensive, especially when spring storms occur. The benefit, however, is enhanced reproductive success.

### 3.1 Modulation of the adrenocortical response to stress

There is extensive evidence that birds can adjust the responsiveness of the HPA axis to the effects of LPFs. To measure responsiveness to stress we take advantage of the fact that capture, handling and restraint of wild birds induces a strong activation of the HPA axis, resulting in a rapid increase in plasma levels of corticosterone within 3 minutes, reaching a maximum by 10–60 minutes. We can collect a small blood sample within 2 minutes. The level of corticosterone in this sample represents the baseline (close to the level just prior to capture). Further small blood samples can then be taken at intervals (e.g. 5, 10, 30 and 60 minutes) to track the increase of corticosterone secretion following the stress of capture, handling and restraint. Examples of this "capture stress" response are given in Fig. 5. It is important to bear in mind that most, if not all, stressors have the potential to elicit increases in corticosterone secretion, although the time, course and extent of the response may be different between reaction to a predator and, for example, a severe weather event (Wingfield, 1994; Wingfield et al., 1995a, b, 1998). The baseline level, the rate of increase of plasma corticosterone levels following capture, and the maximum level attained are measures of the stress response and can be compared across seasons, habitats, ages and genders.

In arctic birds, there is a trend for this responsiveness to decline when birds are breeding (Wingfield, 1994; Wingfield et al., 1995b). Furthermore, this reduced sensitivity to stress appears to be greater in the sex responsible for most parental care (O'Reilly and Wingfield, 2001) and in the most severe environments (Wingfield, 1994). Thus, reduced sensitivity to acute stress when arctic birds are breeding supports our original hypothesis. Moreover, if prolonged severe weather resulted in abandonment of the



nest, then the adrenocortical response to capture stress increased as birds formed flocks roaming the snow-covered tundra (Astheimer et al., 1995). This observation also suggests that responsiveness to stress is suppressed during breeding.

If, however, we now look at the corticosterone response to capture stress in birds arriving on the tundra, we find a different picture. In Gambel's white-crowned sparrow, the response to stress in males actually increased markedly over that recorded in winter, prior to migration (Fig.5, Romero et al., 1997). Eventually, the response to stress would be inhibited as the males progressed into the nesting phase (Holberton and Wingfield, 2003); but on arrival it was greatly enhanced. Note that a non-migratory race of white-crowned sparrow *Z. l. nuttalli*, breeding at mid-latitudes (central coastal California), did not show this type of modulation of the adrenocortical response to stress (Fig.5). Similar enhancement of the response to capture stress at the beginning of the nesting season has now been demonstrated in other avian populations breeding at the northern edge of their range, as in the bush warbler *Cettia di- phone* in Hokkaido, Japan (Wingfield et al., 1995a), the snow bunting and lapland longspur arriving at the northern edge of their range at Thule, Greenland (77°N, J.C. Wingfield et al., unpublished), and arriving red knots *Calidris canutus*, at Alert, Ellesmere Island, Canada (82°N; Reneerkens et al., 2002).

In Gambel's white-crowned sparrow, the increase in adrenocortical sensitivity to stress was accompanied by decreased sensitivity to glucocorticosteroid feedback (Astheimer et al., 1994), and by enhanced sensitivity of adrenal cortex to ACTH

(Romero and Wingfield, 1998), thus producing an overall increase in baseline as well as capture stress induced-plasma levels of corticosterone. This remarkable increase in sensitivity to acute stress contradicts our original hypothesis. However, recent evidence has shown that in birds, as in perhaps most vertebrates, circulating glucocorticosteroids are bound to a protein, corticosteroid-binding globulin (CBG). While bound to this protein, it has been proposed that glucocorticosteroids are largely inactive because they are unable to enter cells and interact with receptors that mediate biological actions (Breuner and Orchinik, 2001, 2002). If this is the case, then it is possible that CBG levels could be modulated, thus buffering such marked increases in responsiveness to LPPs.

#### 4 A corticosterone-binding globulin (CBG) buffer hypothesis

Although the adrenocortical response to acute stress is enhanced at arrival in male Gambel's white-crowned sparrows, there was also an increase in CBG levels that may buffer stress-induced increases in corticosterone; hence the response of free (unbound) corticosterone able to enter cells and interact with receptors was actually reduced (Romero and Wingfield, 1999; Breuner et al., 2003). Thus, although baseline levels of corticosterone, and stress levels after 30 minutes of capture stress, were elevated, high CBG binding capacity of the plasma may actually bind most of this glucocorticosteroid (Fig.5). Indeed, in a comparison of subspecies of the White-crowned Sparrow, it has been shown that the mid-latitude breeding *Z. l. pugetensis* also does not increase responsiveness to stress in early spring, just prior to breeding, and it remains stable throughout the nesting phase

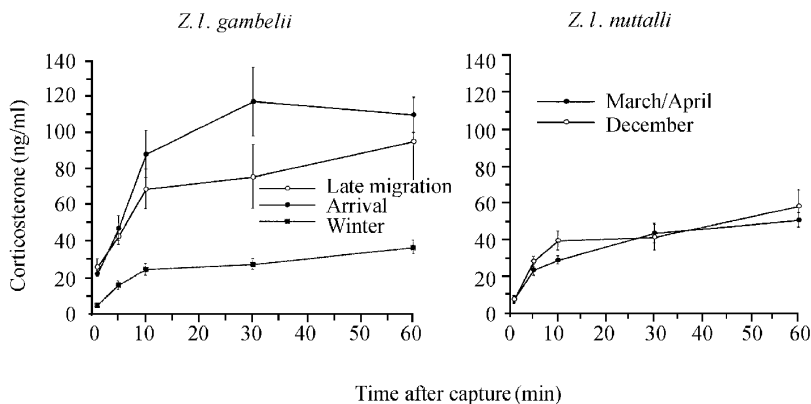


Fig.5 Effects of capture, handling and restraint on plasma levels of corticosterone in free-living white-crowned sparrows *Zonotrichia leucophrys*

The left hand panel shows seasonal changes in hormone response to capture stress in *Z. l. gambelii*. Note that during migration (in central Alaska), the baseline and maximum plasma levels of corticosterone increase, with a further elevation of maximum levels on arrival on the breeding grounds at Toolik Field Station. In the right hand panel, the hormonal response to capture stress shows no such seasonal change in non-migratory *Z. l. nuttalli* sampled at Bodega Bay, central California.

(J. C. Wingfield, unpublished). Lower binding capacity of CBG measured in *Z. l. pugetensis* sampled later in the season may actually result in higher free levels of corticosterone 30 minutes post-capture than in *Z. l. gambelii* (Breuner et al., 2003). If plasma levels of corticosterone, CBG binding capacity, and affinity for corticosterone are known, then free corticosterone levels in blood can be calculated to give an estimated level of potentially biologically active steroid (Breuner et al., 2003). Such a calculation shows that at least during the nesting phase, and despite higher baseline and 30 minute post-capture stress levels of corticosterone in *Z. l. gambelii* males, the free levels are actually reduced compared to those in samples of male *Z. l. pugetensis* collected at a similar phase (Breuner et al., 2003). These data are consistent with our hypothesis that the adrenocortical response to stress, at least in terms of the free level of hormone generated in response to a LPF, is actually reduced.

There is precedent for this kind of regulation in other avian species. In the house sparrow *Passer domesticus*, seasonal changes in adrenocortical responses to capture stress are buffered by changes in CBG binding capacity of plasma so that the free level of corticosterone 30 minutes post-capture does not change (Breuner and Orchinik, 2001, 2002). So why show seasonal modulation of the adrenocortical response to stress (LPFs) and then buffer the response by modulating CBG binding capacity in blood? It is possible that the buffering action of CBG may maximize flexibility of metabolic and behavioral responses to LPFs at different times of the year. For this to work, CBG levels in blood should be regulated as well, especially for short-term finely-tuned free levels of corticosterone that are then able to enter cells and bind to receptors (Breuner and Orchinik, 2002).

There is recent evidence that CBG binding capacity may be regulated within hours if a LPF persists. In captive male *Z. l. gambelii*, food restriction (to mimic the effects of a storm that covers food resources) increased plasma corticosterone levels for 2 hours but had no effect on CBG binding capacity. After 22 hours of food restriction, corticosterone levels matched those of the controls, but CBG levels had declined significantly, thus increasing free corticosterone titers (Lynn et al., 2003). In this scenario we see a fairly rapid (within 2 hours) response to food restriction, even before major metabolic stress has set in, after which CBG levels declined as the period of food restriction persisted, thus releasing corticosterone to increase the free levels above those of controls.

Clearly, the hormone-behavior system associated with arrival biology is highly flexible, allowing an ap-

parent adrenocortical response to LPFs but buffering the early effects with high initial CBG binding. If an LPF persists, then a decline in CBG releases corticosterone into cells. Although much more work needs to be done to assess how quickly the changes in CBG binding capacity can occur, this may be a very elegant system by which migrant birds arriving on the arctic tundra, or other habitats, may retain the activity of the HPA axis intact, but modulate the expression of the CBG gene (or down-stream translation of that gene) and thus access of hormone by receptors. The next question is: are corticosterone receptors also modulated in migrant birds arriving in the Arctic?

## 5 Corticosteroid receptors in target tissues

Before the question of cellular receptor regulation for corticosterone can be answered, it is necessary to describe the types of receptors present in the tissues of passerine birds. In mammals, there are two genomic receptors: the high affinity, mineralocorticoid (MR) receptor activated at basal (normal) levels, and the low affinity, glucocorticoid (GR) receptor activated at higher "stress" levels. Evidence to date suggests that a similar system operates in passerines (Breuner and Orchinik, 2001; Breuner et al., 2003). *In vitro* binding experiments show that the MR-like receptor in sparrows has high affinity binding for corticosterone (as in mammals) but has different specificity characteristics, suggesting the sparrow receptor might be different from the mammalian one (Breuner et al., 2003). However, the GR-like receptor with a lower binding affinity for corticosterone does appear to be similar in specificity to that of mammals (Breuner and Orchinik, 2001; Breuner et al., 2001, 2003). Both MR-like and GR-like intracellular receptors for corticosterone were found in the brain and liver of house sparrows and three taxa of white-crowned sparrow (Breuner et al., 2003). Because the higher levels of corticosterone in response to LPFs are of primary interest here (they mediate the physiological and behavioral components of the ELHS), we now focus on the GR-like receptor because it is only activated at higher circulating concentrations of corticosterone.

There were no significant differences in the binding capacity of GR-like receptors in either the liver or the brain of *Z. l. gambelii* (arctic-breeding) or of *Z. l. pugetensis* (mid-latitude-breeding) males. Because the plasma level of corticosterone, CBG binding capacity, and MR-like receptor capacity were measured, this provides a general model of corticosterone action, estimating the number of receptors occupied at given free corticosterone levels. Using mean levels of free corticosterone and GR-like receptor capacity, the receptor occupancy during

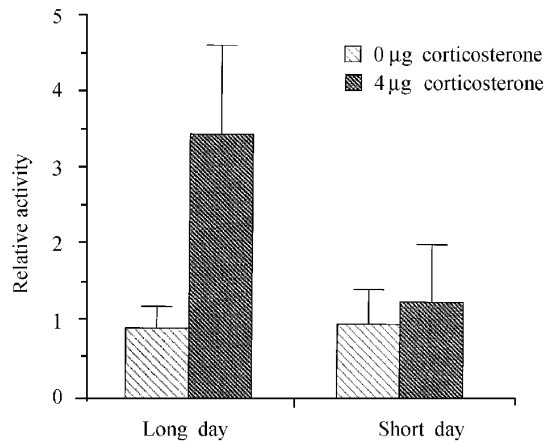
stress can now be calculated. Although the binding capacity of GR-like receptors did not vary between the two taxa of white-crowned sparrow, there did appear to be more GR-like receptors occupied by corticosterone 30 minutes post-capture in both liver and brain of *Z. l. pugetensis* (Breuner et al., 2003). These data strengthen the argument that CBG buffering actually decreases sensitivity to LPFs in arriving *Z. l. gambelii*.

There is also a putative non-genomic receptor mediating more rapid effects of glucocorticosteroids, within minutes (Breuner et al., 1998). Male white-crowned sparrows fed meal worms injected with known doses of corticosterone showed elevated plasma levels of corticosterone within 15 minutes of ingestion. Ingested corticosterone was cleared by 1 hour post-ingestion, thus mimicking a transient LPF that activates the HPA axis. Behavioral observations indicate that this non-invasive way of administering corticosterone results in an increase in perch-hopping activity within about 10 minutes, compared with controls. Such rapid action is not consistent with genomic receptors that require at least 30 minutes and usually several hours to react (Breuner et al., 1998; Breuner and Orchinik, 2002; Orchinik et al., 2002). Interestingly, the lower dose of corticosterone consistent with intermediate plasma levels was effective, but not a higher dose consistent with high stress levels (Breuner et al., 1998). Therefore, it is possible that rapid, non-genomic effects of corticosterone on activity may be important in arriving birds that are not subjected to severe LPFs. Furthermore, the actions of this membrane-type receptor appear to be greatest in spring, when arrival occurs, and less so in winter (Fig. 6, Breuner and Wingfield, 2000), suggesting that such rapid effects on activity may be related specifically to arrival biology and perhaps also the onset of breeding.

## 6 Mechanisms underlying arrival biology of migrant birds in the Arctic

Cumulatively, data suggest that the adrenocortical response to stress is increased on arrival in spring concomitant with reduced sensitivity to glucocorticosteroid feedback and enhanced adrenal sensitivity to ACTH. However, elevated binding capacity of CBG buffers this increase so that free circulating levels of corticosterone are actually reduced. Binding capacity of the GR-like genomic receptors for corticosterone does not appear to differ in the brain or liver tissue of *Z. l. gambelii* compared with *Z. l. pugetensis*. Yet despite higher baseline concentrations of corticosterone in arriving *Z. l. gambelii*, CBG buffering action can cause the numbers of GR-like receptors occupied to actually fall after 30 minutes of post-capture

stress. Additionally, we have shown that levels of CBG (measured as binding capacity in plasma) can also be regulated over 24 hours if an LPF persists. Thus, although the adrenocortical response to stress is elevated in arriving migrants in the Arctic, the effective free level of corticosterone is reduced compared with that in congeners at mid-latitudes. Furthermore, the binding dynamics of both CBG and GR-like receptors in tissues may result in fewer genomic receptors being occupied than originally thought. Counter this with independent regulation of CBG binding and there emerges a highly flexible system fine-tuning an individual's response to an LPF, either towards more resistance (favoring establishment of a territory and onset of breeding) or greater sensitivity (favoring retreat to a refuge and delayed onset of breeding).



**Fig. 6** Modulation of non-genomic receptor activity for corticosterone in white-crowned sparrows *Zonotrichia leucophrys gambelii* as indicated by behavioral responses to non-invasive administration of corticosterone

Only on long days (similar to time of breeding) was corticosterone able to increase activity rapidly. From Breuner and Wingfield (2000).

There may also be adaptations of the hormone-behavior systems that do not involve stress modulation. The rapid acting non-genomic receptor effect on activity appears to be effective at baseline levels of circulating corticosterone, and only in long-day male *Z. l. gambelii*, at a stage equivalent to arrival in the field. The increase in perch-hopping activity may be related to final stages of spring migration in the Arctic when birds arrive on their breeding grounds, locate suitable breeding habitat, and familiarize themselves with immediate food sources should conditions deteriorate and conceal them. Stress levels of corticosterone, as generated by subcutaneous implants of corticosterone in the absence of food, also increase perch-hopping activity as well as escape-type behavior in male *Z. l. gambelii* (Astheimer et al., 1992). This behavior is different from that observed by Bre-

uner et al. (1998), and is perhaps consistent with leaving the area (irruptive migration) sometimes seen in response to severe and prolonged LPFs (Wingfield, 2003). But, how would one hormone, corticosterone, regulate both types of activity? Certainly different receptor types may be involved, but further evidence suggests that irruptive behavior, and its perch hopping equivalent, is also influenced by CRF injected centrally into the third ventricle of male *Z. l. gambelii* in the laboratory (Maney and Wingfield, 1998), as well as by central injections of CRF into the lateral ventricles of male *Z. l. gambelii* in the field (Romero et al., 1998). Thus corticosterone action may play a permissive role for secretion of brain peptides, or other substances, to provide specific behaviors for particular environmental scenarios. Further research will determine whether such interactions occur in the regulation of activity associated with arrival biology.

Although much more research needs to be done, the concept of arrival biology of migrant birds is emerging. Additionally, we have the beginnings of a scheme for the hormonal regulation of the behavior and physiology of this phenomenon. There appears to be a highly flexible control system that allows migrants to respond rapidly and adaptively to a highly unpredictable environment, thus maximizing fitness by allowing them to settle on suitable habitat and begin breeding as soon as possible. Yet more hormone-behavior adaptations may be found, particularly in relation to actions of sex steroids such as testosterone on territorial aggression and pair formation. Obviously, the study of arrival biology of migrant birds involves a highly integrative mix of behavioral, physiological and landscape ecology, and organismal, cell and molecular endocrinology.

## 7 Future directions

Much remains to be revealed in the hormone-behavior interrelationships of and ecological factors associated with arrival biology. Are there additional hormone systems involved, and do different species integrate the physiology and behavior of arrival in similar or different ways? The arrival biology of migrant birds can be studied in other regions on the earth, such as mountains, deserts and mesic habitats. Are similar control mechanisms in place, and do these differ from the well-studied examples of stopover biology during migration in spring and autumn? The arrival biology of migrant birds at their wintering areas in autumn should also be of interest, as it is likely to be rather different from that in spring.

Other intriguing questions include: what are the environmental cues triggering changes in CBG, genomic and membrane receptors associated with arrival

biology? Will global climate change increase environmental unpredictability, making phenotypic flexibility a critical factor in dealing with long-term changes in the environment? Can arctic animals adjust accordingly? Will the highly plastic hormone-behavior interaction system underlying arrival biology enable them to cope? It is hoped that this paper will have heuristic value in characterizing the phenomenon of arrival biology. The possibilities for truly integrative research from molecules to populations are challenging.

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