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Weathering the storm: Do arctic blizzards cause repeatable changes in stress physiology and body condition in breeding songbirds?

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ABSTRACT

Severe weather events are increasing worldwide because of climate change. To cope with severe weather events, vertebrates rely on the stress response which is activated by the hypothalamic-pituitary adrenal (HPA) axis to adjust physiology and behavior. Previous studies have detailed changes in baseline concentrations of the stress hormone corticosterone during a single storm event, but little data exists on how stress physiology and body condition are adjusted as the storm progresses across multiple days. This represents a serious gap in our understanding of how birds respond physiologically over the duration of a storm. We documented arctic snowstorms that occurred over five consecutive years that were endured by Lapland longspurs (*Calcarius lapponicus*; 2012–2016) and in three consecutive years by white-crowned sparrows (*Zonotrichia leucophrys gambelii*; 2014–2016). Data were collected on storm-free days, during snowstorms ranging in length from 1 to 3 days, and the day immediately following a snowstorm. The specific aims were to understand how stress physiology, measured at baseline and in response to restraint handling, and body condition changed over multiple days of the storm, and if these responses were consistent across years. Snowstorms did not affect baseline corticosterone concentrations for either species except for female Lapland longspurs and male white-crowned sparrows in 2014. Lapland longspurs, regardless of sex, increased stress-induced (restraint handling) corticosterone in response to snowstorms in all years but 2013, which was characterized by unusually harsh conditions. Both sexes of White-crowned sparrows showed a significant increase in the stress-induced levels of corticosterone during snowstorms in one of the three years of the study. Stress-induced corticosterone concentrations were only different across each day of the storm in one year of the study for Lapland longspurs. Changes in fat and body mass were not uniform across years, but measurable increases in fat stores and body mass were detected in males of both species during the first day of a snowstorm with declines typically occurring by the second day. Our study showed that severe weather events often caused rapid increases in HPA axis activity and body condition, but these profiles are likely dependent upon ecological and environmental context within the breeding season.

1. Introduction

When migratory songbirds arrive on their breeding grounds they face many environmental challenges that vary from year to year such as predation, snow cover, severe weather, social instability, and food shortages (Newton, 2006; Wingfield et al., 2015). Each of these factors can cause physiological and/or psychological stress that disrupt homeostasis. Birds, like other vertebrates, rely upon the activation of the hypothalamic-pituitary adrenal (HPA) axis, including the production of glucocorticoids, to regulate physiology and behavior and restore homeostasis following an environmental perturbation (Sapolsky, Romero and Munck, 2000; Romero and Wingfield, 2015). Circulating levels of corticosterone can fluctuate between baseline and stress-induced levels, the latter often experimentally studied via restraint handling (Romero, 2002; Wingfield and Sapolsky, 2003). Baseline levels of corticosterone act primarily through high affinity mineralocorticoid receptors (MR), while stress-induced concentrations act on low affinity glucocorticoid receptors (GR) (Joëls et al., 2008; de Kloet,

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2014). This creates a two-tier system of receptor activation by which physiology and behavior can be modified based on the level of HPA axis activation (Sapolsky, Romero and Munck, 2000; Angelier and Wingfield, 2013; de Kloet, 2014).

Studies across taxa have shown that HPA axis activity is highly plastic and is modulated according to life history stage (i.e., breeding, molt, migration, winter) (Astheimer, Buttemer and Wingfield, 1994; Romero, Soma and Wingfield, 1998b; Reneerkens et al., 2002; Romero, 2002; Holberton and Wingfield, 2003; Meddle et al., 2003; Krause et al., 2015b,c; Walker et al., 2015). In many species, both baseline and stress-induced corticosterone concentrations are higher during the breeding season than any other time of the year (Romero, 2002). Taken together, these findings suggest an evolutionarily conserved process by which endocrine set points are adjusted throughout the annual cycle to meet energetic demands associated with each life history stage. For instance in birds, baseline levels of corticosterone likely vary in a nonlinear fashion with parental investment: moderate levels of baseline corticosterone increase parental care, while high levels reduce or terminate parental care (Wingfield, Moore and Farner, 1983; Raouf et al., 2006; Bonier et al., 2009; Spée et al., 2010; Ouyang, Quetting and Hau, 2012; Thierry et al., 2013; Vitousek, Jenkins and Safran, 2014; Ouyang et al., 2015). Corticosterone has been proposed to be an important mediator of life history trade-offs between survival and reproduction because of this relationship (Wingfield et al., 1998). Prolonged elevation of corticosterone can cause the individual to redirect available energetic resources towards self-maintenance and abandon other activities such as breeding, a suite of responses termed the "emergency life history stage" (Wingfield, O'Reilly and Astheimer, 1995; Wingfield et al., 1998; Angelier and Chastel, 2009). The threshold for triggering the emergency life history stage is thought to fluctuate across both seasonal activities and an individual's life-time due to the associated fitness cost of abandoning the current life history stage (Wingfield and Kitaysky, 2002).

HPA axis activity, as measured through baseline and stress-induced corticosterone levels, has been shown to increase during inclement weather (Smith, Wingfield and Veit, 1994; Raouf et al., 2006; Krause et al., 2016a). For migrants and resident species breeding in the Arctic, snowstorms are a common type of severe weather event that can occur at any point during the summer. With climate change, severe weather events are occurring more often and are predicted to continue to increase in frequency (Smith, 2011; Wingfield et al., 2017). Snowstorms are energetically challenging as snow cover reduces access to food and low temperatures increase thermoregulatory costs (Kendeigh, 1969; Astheimer, Buttemer and Wingfield, 1995; Krause et al., 2016a). As a consequence, if negative energy balance occurs, fuel stores are mobilized to meet energetic demands (likely through corticosterone signaling), which results in a decrease in body condition (Landys, Ramenofsky and Wingfield, 2006; Krause et al., 2017). The influence of just a single storm event has been shown to elevate both baseline (a sample collected within three minutes of capture) (Wingfield, Moore and Farner, 1983; Smith, Wingfield and Veit, 1994; Astheimer, Buttemer and Wingfield, 1995; Jenni-Eiermann et al., 2008) and stress-induced levels (measure over a 1 h sampling period) (Krause et al., 2016a) of corticosterone. In addition, the duration of the storm (in days) may influence the magnitude of these changes (Wingfield, 1985b; Wingfield, 1985a; Angelier and Wingfield, 2013). Elevated corticosterone levels have been correlated with promoting escape behavior (Breuner and Hahn, 2003; Lynn, Breuner and Wingfield, 2003) and foraging (Astheimer, Buttemer and Wingfield, 1992), as well as additional behavioral and physiological adjustments such as changes in antipredator behavior (Cockrem and Silverin, 2002; Jones et al., 2015) and immunological alterations (Sapolsky, Romero and Munck, 2000). Failure to respond appropriately to a stressor, in this instance a snowstorm, may result in decreased lifespan and/or reproductive output (McEwen and Wingfield, 2003; Angelier and Wingfield, 2013).

Previous studies on storm events have only described hormonal responses, typically baseline concentrations, during a single storm event (1 day) while not accounting for how physiology and body condition might be adjusted as the storm progresses across multiple days. This represents a serious gap in our understanding of how birds respond to unpredictable events and whether there is a unifying pattern of hormonal signaling and changes in body condition when the emergency life history stage is activated. We studied Lapland longspurs (*Calcarius lapponicus*) from 2012 to 2016 and Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*) from 2014 to 2016 on their breeding grounds in the vicinity of Toolik Lake Research Station, in the Low Arctic tundra ecosystem of the North Slope of Alaska, USA. Both species have been well characterized with regards to their breeding biology and stress physiology in the Low Arctic and how they respond behaviorally and physiologically to both severe and benign conditions (Astheimer, Buttemer and Wingfield, 1995; Krause et al., 2015c; Krause et al., 2016a). Data collected at Toolik Lake indicate that average local spring temperatures have not changed in the last thirty years despite measurable changes at other arctic sites (Hobbie et al., 2017). However in the Toolik area thawing degree days have increased 23% over the past 50 years and peak stream discharge rates, which are often used as a proxy for spring snowmelt, indicate snowmelt is occurring earlier in the spring by 1.8 days per decade over the past 40 years (Tape et al., 2016). Other changes include the occurrence of snow fall in the spring appearing to be shifting later in the year indicated by a study in the Canadian Arctic (Nelson et al., 1997; Xiaogang, Philip and Daqing, 2015). In each year of this study, snowstorms occurred in late May or early June, providing us with an unprecedented five years of data on Lapland longspurs and three years on white-crowned sparrows. The goals of this study were to understand 1) if physiology and body condition changed in response to severe snowstorms, 2) if these responses changed over the duration of the storm and immediately after its conclusion, 3) if the responses differed by sex and species, and 4) if these responses were repeatable at the population level across years. We predicted that both baseline and stress-induced corticosterone would be elevated during snowstorms, that body condition would decline over the duration of the storm, and that these responses would be repeatable across years. A basic understanding of all these factors will give us a mechanistic understanding of how organism will cope with a world that is experiencing an increase in extreme weather events.

2. Materials and methods

2.1. Study Site, Species, and phenology

This study was conducted from 2012 to 2016 during May and June at Toolik Lake Field Station (N 68° 38′, W 149° 36′), located in the foothills of the Brooks Range on the North Slope of Alaska, USA. Lapland longspurs and Gambel's white-crowned sparrows are long-distance migratory songbirds that winter in the contiguous United States and breed at higher latitudes (Blanchard and Erickson, 1949; West, Peyton and Irving, 1968). Lapland longspurs are arctic specialists that have a circumpolar breeding distribution and nest in tussock and polygon tundra (Boelman et al., 2014; Walker et al., 2015). Gambel's white-crowned sparrows are thought to be more recent colonizers of the Low Arctic and primarily breed throughout the boreal forest (Krause et al., 2015a). In the Low Arctic, white-crowned sparrows prefer to nest on tundra dominated by deciduous woody shrubs and evergreens (Boelman et al., 2014; Boelman et al., 2016). Spring phenology of the breeding life history stage can be divided into sub-stages including arrival on breeding grounds, territoriality, clutch initiation and incubation and have been outlined in detail in Boelman et al. (2017). Both species typically arrive ("arrival period") on the breeding grounds between the first and third week of May, depending on environmental conditions. Conditions upon arrival are characterized by extensive snow cover, patchy resource availability, low ambient temperatures, and reduced shelter (Custer and Pitelka, 1977; Boelman et al., 2017).