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Stress responses and disease in three wintering house finch (*Carpodacus mexicanus*) populations along a latitudinal gradient

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Abstract

In laboratory studies, stress hormones have been shown to impair immune functions, and increase susceptibility to diseases. However, the interactions between stress hormones and disease have rarely been studied in free-ranging populations. In this study, we measured concentrations of the avian stress hormone corticosterone across four winter months (December–March) over two years in three eastern North American house finch populations (*Carpodacus mexicanus*) along a latitudinal gradient. Because *Mycoplasma gallisepticum* infections appear in these populations in late winter, we hypothesized that the timing of the disease outbreaks could be mediated by changes in corticosterone concentrations. We found a significant increase in baseline and stress-induced plasma corticosterone concentrations in house finches without *Mycoplasma* symptoms in late winter; when the prevalence of *Mycoplasma* infection peaks. We also found that house finches with *Mycoplasma* symptoms had elevated stress-induced corticosterone concentrations. High baseline concentrations were associated with a low body condition and a high fat load. We found that the relationship between corticosterone concentrations and the latitude of the study population changed between years. The first year, corticosterone concentrations were lowest in the southern latitude, but became higher in the second year when average winter temperatures were low. A causal understanding of the implications for this variation in corticosterone concentrations for *Mycoplasma* disease dynamics awaits further studies.

Keywords: *Carpodacus mexicanus*; House finch; Stress; Corticosterone; *Mycoplasma gallisepticum*; Latitude; Infection

1. Introduction

Although the majority of vertebrate species that have been studied have been found to modulate their stress responses seasonally (Romero, 2002), it is not clear why these seasonal modulations occur. Several ideas have been put forward that could explain how modulations of stress responses could be adaptive (reviewed in Romero, 2002). First, glucocorticosteroid rhythms have been suggested to reflect variation in the energy balance of an organism. Thus, when energetic needs exceed the available amounts of energetic resources, glucocorticosteroids will become elevated (Goymann and Wingfield, 2004). Second, the frequency of exposure to stressors could vary with the seasons. If, for example, competition for mates is more intense in the breeding season, this could lead to increased stress responses at this time of the year (Sapolsky et al., 2000). And third, the need to respond to a stressor can vary over the season. While it may be adaptive to respond strongly to a stressor and abandon the territory when there are many alternative options, it may be more beneficial to stay when the alternative options are few (Wingfield, 1994).

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Glucocorticoid concentrations can also vary between populations living at different latitudes. A study by Silverin et al. (1997) found that willow warblers (*Phylloscopus trochilus*) in northern Sweden had lower magnitudes of stress responses than those from a population further south. This observation led to the suggestion that stress responses in birds were down-regulated at higher latitudes to prevent nest abandonment when breeding seasons were short, and the alternative options were few. However, other studies have found the opposite pattern with high responses at high latitudes in both breeding and wintering birds (Holberton and Able, 2000; Wingfield et al., 1995). High corticosterone concentrations in the winter could be expected because birds that over-winter in colder climates have greater energetic demands and live in a less predictable environment. A stronger stress response might therefore be required to respond to changes in energy demands and food availability. Thus, it has become clear that just like seasonal differences, differences in glucocorticoid responses between populations can occur for many reasons, and several models may be required in order to explain differences between populations on different latitudes and within populations at the same latitude (Breuner et al., 2003; Romero, 2004).

Life-history theory provides an alternative approach to understand seasonal and latitudinal variation in stress responses. Because an organism's physiological resources are limited, investments of resources like energy and nutrients have to be balanced between competing demands (Ricklefs and Wikelski, 2002). In this framework, hormones like corticosterone may serve as mediators that re-allocate limited resources across different functions. Because the maintenance of an immune defense is physiologically costly (Bonneaud et al., 2003; Martin et al., 2003), and stress hormones have several down-regulatory effects on immune functions (Apanius, 1998; Nelson et al., 2002), an up-regulation of the stress response can be viewed as an adaptive re-direction of resources away from the immune system to meet more urgent demands (Lochmiller and Deerenberg, 2000; Sheldon and Verhulst, 1996). Observations that immunity in passerines is compromised during energetically demanding activities, such as reproduction, have lent support to this view (Lochmiller and Deerenberg, 2000; Zuk and Stoehr, 2002).

In this study, we investigated the variation in corticosterone concentrations in free-ranging house finches (*Carpodacus mexicanus*) at three different latitudes. We studied three eastern populations of house finches that during the last decade have been subject to regular outbreaks of infections caused by the bacterium *Mycoplasma gallisepticum*. We were interested in quantifying the variation in stress responses between years, winter months and latitudes in house finch populations. This would allow us to explore the hypothesis that seasonal modulation of the stress response could impacts disease dynamics in this study system.

House finches infected with *Mycoplasma* first appeared on the North American east coast in 1994, and since then the disease has spread rapidly in house finch populations across the country and reduced the abundance of house finches in affected areas (Hochachka and Dhondt, 2000). Because the disease can be visually detected, *Mycoplasma* infection in house finches has become a model system for the study of emerging disease in wildlife (Dhondt et al., 2005). From the long-term data set that has been collected, it has become clear that the variation in *Mycoplasma* prevalence has a strong seasonal component, and the proportion of infected individuals show peaks in the late summer and late winter (Altizer et al., 2004).

Seasonal variations in disease prevalence are common and can be caused by both extrinsic factors such as climate, or intrinsic factors such as changes in host immunity (Nelson et al., 2002). Several hormones can influence immune functions, but some of the more potent immuno-modulators are the glucocorticoids that are released by the hypothalamic–pituitary–adrenal (HPA) axis during stress (Apanius, 1998). The interaction between the stress hormones of the HPA axis and the immune system have been studied extensively in the laboratory, but few studies have examined this link in wildlife populations (Nelson et al., 2002).

In this study, we measured monthly mean corticosterone concentrations in three free-ranging house finch populations in two winter seasons (December–March), at a time of the year when we expected the prevalence of *Mycoplasma* infection to increase. We examined the yearly, monthly, and latitudinal patterns of variation in stress responses between populations. We also examined if the sex, body condition or infection status could explain variation in stress responses between individuals.

2. Materials and methods

2.1. Study species and populations

The house finch is a small (20 g) North American Cardueline finch (Badyaev, 2003). In the winter, house finches aggregate in large feeding flocks, and their diet consists primarily of seeds (Hill, 1995). In the spring, the winter feeding-flocks disperse and house finches form breeding pairs. Male song and pair formation becomes evident in January in the southern latitudes and in February in northern latitudes (Hill et al., 1999). The breeding season of house finches is extended, and covers a period of six months in which pairs can fledge between 2 and 5 broods (McGraw et al., 2001). Finally, house finches are partial migrants, and some birds leave their breeding area in the autumn and over-winters in milder climates (Hill, 1993).