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## Life-history dependent relationships between body condition and immunity, between immunity indices in male Eurasian tree sparrows

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### ABSTRACT

In free-living animals, recent evidence indicates that innate, and acquired, immunity varies with annual variation in the demand for, and availability of, food resources. However, little is known about how animals adjust the relationships between immunity and body condition, and between innate and acquired immunity to optimize survival over winter and reproductive success during the breeding stage. Here, we measured indices of body condition (size-corrected mass [SCM], and hematocrit [Hct]), constitutive innate immunity (plasma total complement hemolysis activity [CH<sub>50</sub>]) and acquired immunity (plasma immunoglobulin A [IgA]), plus heterophil/lymphocyte (H/L) ratios, in male Eurasian tree sparrows (*Passer montanus*) during the wintering and the breeding stages. We found that birds during the wintering stage had higher IgA levels than those from the breeding stage. Two indices of body condition were both negatively correlated with plasma CH<sub>50</sub> activities, and positively with IgA levels in wintering birds, but this was not the case in the breeding birds. However, there was no correlation between CH<sub>50</sub> activities and IgA levels in both stages. These results suggest that the relationships between body condition and immunity can vary across life-history stage, and there are no correlations between innate and acquired immunity independent of life-history stage, in male Eurasian tree sparrows. Therefore, body condition indices predict immunological state, especially during the non-breeding stage, which can be useful indicators of individual immunocompetences for understanding the variations in innate and acquired immunity in free-living animals.

### 1. Introduction

A functioning immune system is essential to survival because it provides fundamental protection against potentially fatal parasites and pathogens (Schmid-Hempel and Ebert, 2003). Immune systems are, however, energetically expensive to maintain and this cost must be balanced against the fitness benefits of other physiological activities such as reproduction (Hasselquist and Nilsson, 2012; Klasing, 2004; Ricklefs and Wikelski, 2002). This means that, in order to maximize fitness, there is a trade-off between allocating resources to the immune system as opposed to other physiological and behavioral requirements (Hasselquist and Nilsson, 2012; Martin et al., 2008).

Reduction in indices of immune function have been documented in all phases of the life history of free-living animals, including reproduction and over-wintering (Hegemann et al., 2012). Several hypotheses have been proposed to explain this (Hegemann et al., 2012). For example, the winter immune-enhancement hypothesis proposes that

animals should upregulate the immune system in the non-breeding stage when they are relatively inactive, but downregulate it while breeding because of the high energetic cost of reproduction (Hasselquist, 2007; Martin et al., 2008; Nelson et al., 2002). However, the antigen-exposure hypothesis proposes that immunity should increase during the breeding stage, because of the higher risk of infection during that period (Hasselquist, 2007; Møller et al., 2003). Recent evidence shows that immunity can vary with the demand for, and availability of, food resources over the course of a year (Hegemann et al., 2012, 2013; Martin et al., 2008). Understanding how animals fine-tune their immune system during different life-history stages is an essential first step towards uncovering the underlying trade-offs between competing physiological requirements.

Animals require sufficient energy and nutrients to develop, activate, and maintain their immune system. Previous studies have shown that the immune system is affected by, and dependent on, the relative body condition of an individual; i.e. depleted energy reserves can impair

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immunity (Demas et al., 2003; Moore et al., 2011; Nussey et al., 2014; reviewed by Lochmiller and Deerenberg, 2000). In free-living animals, body condition, including body mass and size-corrected mass (SCM), are often used as an estimate of the energetic (or nutritional) state of individuals, especially the relative size of its energy reserves and fitness (Green, 2001; Merilä and Wiggins, 1997; Peig and Green, 2009). In addition, hematocrit (Hct) is an indicator used to assess changes in oxygen carrying capacity necessitated by fluctuations in metabolic demands, which is also regarded as an indicator of individual quality and fitness (Fair et al., 2007; Williams, 2012). Generally, higher Hct levels are associated with the increased energetic demands of physiological activity (Fair et al., 2007; Williams, 2012), whereas low Hct is associated with poor nutrition and parasitism (Fair et al., 2007; Richner et al., 1993). In free-living birds, body condition, Hct and immune function all vary with life history stage (Krause et al., 2016; Wojczulanis-Jakubas et al., 2015) which suggests that the allocation of resources to the immune system or to body condition should also vary with life-history stage (Martin et al., 2008).

The immune system is comprised of the innate, and acquired, immune subsystems. The innate immune subsystem includes anatomical barriers, anti-microbial soluble proteins (e.g. complement activity), and natural killer cells, which defend against a wide range of pathogens. In contrast, the acquired immune subsystem is comprised of highly specialized cell-mediated and humoral components, such as systemic cells and processes (e.g. immunoglobulins secreted by B cells), that eliminate or prevent the growth of specific pathogens (Alberts et al., 2002). Trade-offs between these two subsystems have been documented in both birds and mammals in which individuals generally have either a strong innate, or strong acquired, immune system, but not both (Lee et al., 2008; Martin et al., 2007). However, little is known about the relationship between innate and acquired immunity in relation to life-history stage. This information is critical to understanding how free-living animals fine-tune the relationships between immunity and body condition, and between innate and acquired immunity, so as to optimize their chances of survival during the non-breeding stage, and of successful reproduction during the breeding stage (Hasselquist and Nilsson, 2012; Hegemann et al., 2012; Lee, 2006; Martin et al., 2008).

Life history theory assumes that individuals with better body condition can invest more in reproductive effort, thereby increasing their reproductive output relative to those in poorer condition (Ricklefs and Wikelski, 2002). This is especially true for short-lived species, although maintaining high levels of reproductive-related hormones and energetically expensive reproductive behavior is costly (Ricklefs and Wikelski, 2002). Recently, assessment of multiple immune indices has become more common in eco-immunology as a means of understanding variations in innate and acquired immunity, how these relate to different life history phases and are influenced by an individual's physiological state.

The Eurasian tree sparrow (*Passer montanus*), is a relatively short-lived, seasonally breeding species that is widely distributed across the Eurasian continent. Previous studies have demonstrated that the body condition of Eurasian tree sparrows varies with life history stage (Li et al., 2012), and those individuals with better body condition during breeding stage have lower heterophil/lymphocyte (H/L) ratio (Zhang and Zheng, 2007). Furthermore, male Eurasian tree sparrows have significantly higher levels of plasma testosterone (T) and corticosteroid binding globulin (CBG, an index of nutritional status) during early breeding compared to other life history stages (Li et al., 2012, 2017), and those individuals with higher T levels exhibit stronger phytohaemagglutinin skin-swelling (PHA, a measure of both innate and acquired immunity) responses (Li et al., 2015). In the present study, we further test the following hypotheses using male Eurasian tree sparrows: (1) as stated by antigen-exposure hypothesis, Eurasian tree sparrows would enhance their immunity during the breeding stage compared to the wintering stage. (2) there is positive relationship between body

condition and immunity that promotes individual survival during the wintering stage, but which is, to some extent, diminished because greater investment of available resources into reproduction may come at the expense of immunity during the breeding stage. (3) innate immunity is negatively correlated with acquired immunity independent of life history stage. To test these hypotheses, we measured two body condition indices, including SCM and Hct, of male Eurasian tree sparrows during the wintering and the breeding stages, and also determined the constitutive innate immunity index (plasma total complement hemolysis activity [CH<sub>50</sub>]) and acquired immunity index (plasma immunoglobulin A [IgA], as one of the most abundant immunoglobulins, which is positively correlated with body mass, Macpherson et al., 2012; Nussey et al., 2014), and H/L ratios, of these birds. We further correlated body condition and immunological indices to illustrate the life-history dependent relationships between body condition and immunity, and between innate and acquired immunity, that take place in male Eurasian tree sparrows.

## 2. Materials and methods

### 2.1. Experimental protocol and sample collection

Free-living Eurasian tree sparrows were captured opportunistically in mist nets in two sequential life-history stages, the early wintering stage (October 24, 2015) and the early breeding stage (April 28, 2016), on the Hebei Normal University campus (38°01.83'N, 114°31.50'E, elevation: 75 m), Hebei Province, China. The life-history stage of captured sparrows was assumed to be consistent with the timing of their annual cycle, which has been determined by previous studies (Li et al., 2011, 2012, 2015). The Eurasian tree sparrow is sexually monomorphic, therefore, after transfer to the laboratory, birds were sexed by polymerase chain reaction following the procedures described in Round et al. (2007). There are sex differences in Hct levels and immune response in other avian species (e.g. Krause et al., 2016). To avoid the effects of sex difference, subsequent measurements of body condition and immunity indices were performed on male birds only.

Each male sparrow was individually caged (50 × 34 cm in area and 33 cm high), provided with food and water ad libitum, and kept at an ambient temperature of 20 °C. Birds captured in the wintering stage were kept under a photoperiod that stimulated autumn day-lengths (10 L/14D; n = 27), whereas those caught in the breeding stage were kept under a photoperiod that simulated longer, spring day-lengths (14 L/10D; n = 26). Birds were kept under these conditions for 12 to 14 days.

After acclimation, blood samples were collected from all birds by piercing the alar vein with a 26-gauge needle and collecting blood into heparinized microhematocrit capillary tubes. To determine the differential white blood cell count, approximately 5 µl of blood were used to make air-dried whole blood smears using the standard two-slide wedge procedure. Approximately 80 µl of blood samples were collected and stored on ice before being centrifuged at 855g for 10 min. Hct was measured as the relative amount of red blood cells per total blood volume for every capillary tube, then averaged to yield a mean Hct value. Fresh plasma was split into two equal fractions for IgA and CH<sub>50</sub> assays.

After sampling, each bird was weighed to the nearest 0.1 g, and its wing, bill, and tarsus length were measured to the nearest 1 mm. Because of the linear relationships between body mass and morphometric measures, mass/length residuals or a scaled mass index, are often used to estimate the absolute size of energy reserves in free-living animals (Green, 2001; Peig and Green, 2009). However, the relationships between body mass and these morphometric measures in Eurasian tree sparrows were not linear. To estimate relative size of its energy reserves, we calculated SCM using the ratio of body mass (g) to wing length (mm)<sup>3</sup> (Smith et al., 1994). All protocols were approved by the Ethics and Animal Welfare Committee (No. 2013-6), and by the

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