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Innate immunity, assessed by plasma NO measurements, is not suppressed during the incubation fast in eiders

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Abstract

Immunity is hypothesized to share limited resources with other physiological functions and may mediate life history trade-offs, for example between reproduction and survival. However, vertebrate immune defense is a complex system that consists of three components. To date, no study has assessed all of these components for the same animal model and within a given situation. Previous studies have determined that the acquired immunity of common eiders (*Somateria mollissima*) is suppressed during incubation. The present paper aims to assess the innate immune response in fasting eiders in relation to their initial body condition. Innate immunity was assessed by measuring plasma nitric oxide (NO) levels, prior to and after injection of lipopolysaccharides (LPS), a method which is easily applicable to many wild animals. Body condition index and corticosterone levels were subsequently determined as indicators of body condition and stress level prior to LPS injection. The innate immune response in eiders did not vary significantly throughout the incubation period. The innate immune response of eiders did not vary significantly in relation to their initial body condition but decreased significantly when corticosterone levels increased. However, NO levels after LPS injection were significantly and positively related to initial body condition, while there was a significant negative relationship with plasma corticosterone levels. Our study suggests that female eiders preserve an effective innate immune response during incubation and this response might be partially determined by the initial body condition.

Keywords: Body condition; Corticosterone; Fasting; Innate immune response; Lipopolysaccharides; Nitric oxide; Reproductive effort; Trade-off

1. Introduction

Trade-offs between life history components are a central concept in evolutionary ecology. The publication of a paper by Hamilton and Zuk in 1982 [1] generated a considerable interest in the role that parasites might play in the evolution of reproductive strategies. This stimulated the emergence of the field

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of ecological immunology, which investigates the role of immune effector systems in determining host fitness in the wild [2]. The observation that a heavy parasite load during reproduction is associated with a reduced immune response [3] and a decreased adult survival rate [4], led to the hypothesis that immunity must share limited resources with other physiological functions and this may to some extent underpin the costs of reproduction [5].

Recent experiments have indicated that high reproductive effort increases metabolic rate, leading to oxidative stress [6,7] due to increased generation of oxidative metabolites and free radicals [8]. Immunosuppression during reproduction has been viewed as an undesirable consequence of a high metabolic rate [9]. However, even if a high metabolic rate during reproduction might contribute to immunosuppression, it is most likely not the only factor involved [9]. As recently outlined by Viney et al. [10], a ''maximum immune response'' does not necessarily mean that the response is ''optimal'', since an immunosuppression might be of adaptive value [9] and then accepted as a cost by the organism. Firstly, since an activated immunity enhances oxidative stress [8], it carries a non-negligible risk of autoimmune pathology [11,12]. Immunosuppression could therefore be explained by the immunopathology-avoidance hypothesis [9]. In this context, the control of the production of nitric oxide (NO) by immune cells is primordial since overproduction of NO is involved in sepsis shock [13]. Secondly, the resource-limitation hypothesis suggests that different functions compete for limited resources and that investment in costly behaviors, such as reproduction, reduces the amount of resources available to immune defense [9]. This second hypothesis assumes that there is an energetic or nutritional cost associated with the immune system [9,14,15]. However, evidence for an energetically costly immune response is still equivocal [9].

Vertebrate immune defense is one of the most complex biological phenomena. It consists of three components (innate immunity, acquired humoral immunity, and acquired cellular immunity) between which trade-offs may appear [5,10,16–18]. Consequently, multiple immune assays, which challenge different components of the immune system, should be used to gain a better understanding of overall immunocompetence [19]. Since assessment of acquired immunity has proven insufficient for ecological immune studies [16,20], assaying the innate component is of primary importance.

Eider ducks are a useful model for studying the intensity of the immune response in relation to body condition, since females rely solely on their stored body fat during incubation [21]. Previous studies have shown that the acquired immunity of common eider ducks (*Somateria mollissima*) is suppressed during the incubation fast [18,22], and that its experimental activation has strong negative effects on the fitness of female eiders [22]. In fact, immunocompetence may be fixed by fat stores, the main energetic reserves of the organism that determine individual quality of reproductive adults [5,23]. Thus, the decrease in acquired immune response of female eiders can be understood as a consequence of fat stores depletion. However, whether and to what extent eider's whole immune response during reproduction depends on individual quality and is suppressed when body conditions deteriorate is still under debate [24].

Based on these data, we tested whether during the incubation fast, female eiders preserve or not an impenetrable first line of defense. In other words, do eiders maintain a highly effective innate immune response to compensate for the loss of their acquired immune components?

To date, only one study has assessed the constitutive innate immunity by using an *in vitro* assay [25]. We used here an alternative method, commonly used in immunology studies, which is easily applicable to animals in the wild. The innate immune response consists of the activation of phagocyte cells as heterophils and macrophages [26]. Destruction of recognized pathogens by those cells is mainly driven by the production of NO [27], which can be experimentally stimulated by injection of lipopolysaccharides (LPS) [28]. We measured plasma NO concentrations in breeding female eider ducks before and after LPS injection at various stages during their incubation period, while also considering their initial body condition. We assessed body condition by measuring corticosterone levels, an increase in one component being strongly associated with a decline in the other [29,30], and also by calculating a body mass index (mass/tarsus length^3).

2. Material and methods

The study was conducted in a common eider colony on Storholmen Island, Kongsfjorden,