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House sparrows (*Passer domesticus*) adjust their social status position to their physiological costs

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Abstract

For group-living animals, the maintenance of a position in the social hierarchy may be associated with physiological costs such as increased stress and energy expenditure or suppressed immune functions. In this study, we experimentally manipulated the social status of house sparrows so that each bird experienced two social environments in random sequence: being dominant and subordinate. For 14 males, we investigated how corticosterone concentrations, energy expenditure and immune functions were affected by these changes in social status position. We found that the cost of maintaining a social status position differed between individuals and were related to individual body size. Birds with small body size had increased costs in terms of increased stress responses and reduced cell-mediated immune responses while being experimentally kept as dominants, while birds with large body size had increased costs while they were subordinates. We also found that birds with increased energetic and immunological costs as *dominants* obtained a low status position in the large group, while birds with increased costs as *subordinates* obtained a high status position in the large group. In summary, we found that the costs associated with the maintenance of social status position differed between individuals and was related to the individuals' body size. Furthermore, in a large group, individuals maintained a social status position that minimized energetic and immunological costs.

Keywords: Social status position; Physiological cost; Glucocorticoid; Stress; Immunocompetence; *Passer domesticus*

Introduction

Social hierarchies exist among most group-living organisms. The maintenance of a social status position within the group is an important trait for the individual because it determines the priority of access to resources. Because the maintenance of a social status position can be associated with costs (Goymann and Wingfield, 2004), an individual has to balance the potential benefits of maintaining a social status position with the costs. Social status maintenance can be costly because the competitive interactions with other members of the group can induce social 'stress', commonly quantified as an elevation of glucocorticoid hormones released by the hypothalamic pituitary–adrenocortical (HPA) axis (Abbott et al., 2003; Goymann and Wingfield, 2004; Sapolsky et al., 2000; Wingfield et al., 1997). Secondly, an individual's social status can also influence the exposure to stressors, such as starvation or predation. A recent review showed that dominant individuals generally have higher glucocorticoid concentrations compared to those of subordinates in species with cooperate breeding systems (Sands and Creel, 2004, see also Creel, 2001; Creel et al., 1996). A reason for this could be that it is resource demanding to monopolize breeding efforts. In other study systems, like for example winter flocks of birds, glucocorticoid concentrations can instead be higher in subordinate individuals (Creel, 2001; Hegner and Wingfield, 1987). Such patterns could occur because subordinates are more likely to be excluded from food sources or hiding places or because they are harassed by dominants (Barnard et al.,

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1998; Creel et al., 1996; Hegner and Wingfield, 1987; Sloman et al., 2001). Thus, glucocorticoid concentrations can be elevated both in dominants and subordinates under different circumstances.

The finding that, for example, an individual of low status has elevated glucocorticoid concentrations in the field, can have several potential explanations. First, it could be because the maintenance of a low status position is associated with high levels of social stress. Second, the pattern could occur because low status individuals are in poor body condition as a result of their low status. Because an individual's social status position can be related to its physical condition, it is difficult to disentangle cause and effect when investigating correlations between an individual's social status position and glucocorticosteroids concentrations.

Individuals may also differ in their ability to cope with social conflicts (Bartolomuccia et al., 2003; Sapolsky, 1995). Research on primates and birds has emphasized that individuals can have different styles of coping with social stressors, and their individual coping style can influence their response (Carere et al., 2001; Verbeek et al., 1999; Virgin and Sapolsky, 1997). For individuals of a wide variety of species, body size is an important predictor of social dominance because a large body size can be a competitive advantage in physical conflicts (Andersson, 1994). In addition, a large body size can influence an individual's motivation to obtain a dominant social status because individuals with large body sizes have higher absolute energetic requirements (Bryant and Tatner, 1991). Thus, if the availability of resources becomes limited, an individual of large size would reach a negative energetic balance faster than a small animal.

The exposure to stress can be physiologically costly via several pathways. If an elevation of glucocorticoid concentrations is pronounced and persistent, it can impair reproduction (Moore and Jessop, 2003; Wingfield and Sapolsky, 2003) or lead to an increased mortality rate (Romero and Wikelski, 2001). Thus, from an evolutionary perspective, an animal is expected to have evolved behavioral responses to avoid prolonged stress exposure. Chronic stress can be the result of an imbalance in an organism's energy budget (Goymann and Wingfield, 2004) and lead to a down-regulation of the immune system (Apanius, 1998; Hillgarth and Wingfield, 1997) and increased susceptibility to diseases (Barnard et al., 1998; Nelson et al., 2002). Furthermore, relationships between an individual's social status and both energy expenditure (Bryant and Newton, 1994; Hogstad, 1987; Reinertsen and Hogstad, 1994; Senar, 1990) and immune responses or disease resistance (Apanius, 1998; Lindström, 2004; Zuk and Johnsen, 2000) have been found. Because elevation of glucocorticoid hormone concentrations, increased metabolic expenditure and suppressed immunity all represent physiological costs that can be inter-related and because previous studies show inconsistency in regards to which social status position is most costly to maintain, we designed an experiment to disentangle these factors.

Our approach was to perform an experiment on house sparrows (*Passer domesticus*) under standardized conditions in aviaries and measure the costs associated with the maintenance of a dominant and subordinate social status position. The birds in the study were kept isolated before the experiment so that any differences in body condition that may be a result of social status differences would be minimized. We then experimentally manipulated social status and measured corticosterone concentrations, energy expenditure and two types of immune responses both when a bird was in a high and in a low status position. With this approach, we could test several hypotheses.

First, we tested if the maintenance of a certain social status position would be associated with increased physiological costs. If so, we expected to find increased costs (elevated corticosterone levels, increased energy expenditure and suppressed immune responses) in one particular social status position. Because previous studies have shown that both a dominant and a subordinate social status position can be associated with higher costs, we made no a priori prediction of the direction of this relationship.

Second, we tested the hypothesis that birds with a large body size would be better adapted to cope with the social challenge of maintaining a dominant position. Here, we predicted that the physiological cost of maintaining a dominant status position would be related to an individual's body size. Because a large body size can give a competitive advantage, we expected birds of large body size to have a lower cost of maintaining a dominant position compared to small birds.

Finally, we examined if individuals were behaviorally adapted to minimize their physiological cost when the choice of social status position was less restricted. Here, our expectation was that individuals that had experienced increased costs when placed in a dominant social status position in the experiment would reduce these costs by maintaining a low status position in a larger group.

Material and methods

In September and October 2001, 28 experimental male house sparrows were caught in the Princeton area (40,35°N: 74,66°W) using mistnets. After capture, all birds were banded and aged as yearlings or older according to Svensson (1992). We used 18 previously wild caught house sparrows that had been held in captivity for a maximum of 4 months as social partners (see below). After capture, all birds were kept in randomly mixed groups of 5–10 in outdoor aviaries (2 × 2 × 1.5 m). Two weeks before the experiment started, all birds were removed from the aviaries and placed in individual indoor cages (0.5 × 0.5 × 0.4 m) each containing perches and sand. Birds were fed ad libitum, and water was exchanged each day throughout