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Females pay the oxidative cost of dominance in a highly social bird

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Understanding the evolution and maintenance of social behaviour requires a better understanding of the physiological mechanisms underlying the trade-offs between the benefits and costs of social status. Social dominance is expected to provide advantages in terms of access to resources and to reproduction but acquiring and maintaining dominance may also entail physiological costs. Dominant individuals are likely to engage more frequently in aggressive behaviours and/or may allocate a substantial amount of energy and resources to signal their status. Hence, dominance is likely to involve multiple physiological processes that stimulate aerobic metabolism and lead to the generation of reactive oxygen species (ROS). When not depleted, ROS can ultimately lead to oxidative stress. However, the relationship between oxidative status and dominance has seldom been investigated. Here, we examined whether there is a physiological cost, measured as oxidative stress, associated with dominance in a highly social and cooperative bird, the sociable weaver, *Philetairus socius*. Oxidative status was assessed by measuring circulating oxidative damage and the plasma nonspecific antioxidant capacity. We found that in females, but not in males, dominance was associated with higher levels of oxidative damage than in same-sex subordinates, suggesting that the physiological cost of dominance is underpinned by oxidative stress in a sex-specific manner. This associated cost of dominance was independent of previous and future reproductive status. The sex difference in oxidative damage was associated with sex-specific differences in antioxidant defences, with males (the dominant sex) showing higher antioxidant levels than females, independently of their social rank. These findings indicate that social dominance may entail a trade-off between advantages and physiological costs in a sex-specific manner, exposing females to oxidative stress. This scenario may be aggravated during stressful periods, such as drought episodes when food is scarce, and it has implications for understanding female health, ageing and life span.

Conflicts among group members, on whether to compete or share resources, have profound fitness implications by undermining group stability (Ang & Manica, 2010; Poisbleau, Fritz, Guillemain, & Lacroix, 2005) and species have developed a large assortment of behavioural strategies to mitigate such negative aspects of group living. One very common strategy is establishing an order of access to the available resources through dominance hierarchies (Baker, Belcher, Deutsch, Sherman, & Thompson, 1981; Lopez, Muñoz, & Martin, 2002; Meese & Ewbank, 1973; Monnin & Peeters, 1999; Nakano, 1995; Price, 1967; Wittig & Boesch, 2003).

The relative position of an individual within its social environment may have a considerable impact on its fitness. Individuals attaining a higher dominance status are usually those that obtain higher access to or monopolize high-quality resources (e.g. food, territories or breeding opportunities), which may have important positive short- and long-term fitness consequences influencing survival (Price, 1967; White, 2007), dispersal (Chiarati, Canestrari, Vila, Vera, & Baglione, 2011; Gese, Ruff, & Crabtree, 1996) and reproductive success (Côté & Festa-Bianchet, 2001; Nelson-Flower et al., 2011). For example, high-ranking primates appear to have greater foraging efficiency (e.g. female grey-cheeked mangabeys, *Lophocebus albigena*, Chancellor & Isbell, 2009) and energy intake

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rates (e.g. white-faced capuchin, *Cebus capucinus*; Vogel, 2005) than low-ranking ones. In acorn woodpeckers, *Melanerpes formicivorus*, societies, the large and dominant brood mates survive better or are more successful at gaining reproductive opportunities than subordinates (Koenig, Walters, & Haydock, 2011). Low social status, on the other hand, is often viewed as stressful and costly, as subordinate individuals typically endure higher aggression rates, poorer nutrition and suppressed reproduction (Creel, Dantzer, Goymann, & Rubenstein, 2013, and references therein). However, over the last few decades, studies have been showing that attaining a higher dominance rank can also be costly and may have negative impacts on individuals (Creel, 2001; Creel et al., 2013; Hogstad, 1987; Muehlenbein & Watts, 2010; Muller & Wrangham, 2004; Rohwer & Ewald, 1981), particularly when dominance ranks are unstable. Such costs may arise from frequently engaging in energetically and potentially injurious fights or aggressive behaviours in order to maintain a dominant status through 'policing' (Clutton-Brock, Albon, Gibson, & Guinness, 1979; Rowell, 1974), or to obtain access to reproduction (Ang & Manica, 2010; Clutton-Brock et al., 2006; Monnin & Peeters, 1999), while subordinates rarely face such challenges (Creel, 2001; Creel et al., 2013; Sands & Creel, 2004; Sapolsky, 2005). Additionally, the higher rates of reproduction, characteristic of dominant individuals, may impose large energetic and physiological costs linked to demanding activities such as gamete production, mate acquisition and parental investment (Alonso-Alvarez et al., 2004; Anderson & Fedak, 1985; Wiersma, Selman, Speakman, & Verhulst, 2004). Finally, dominant individuals may additionally invest more energy in signalling their status through elaborate colourful patches and other features (e.g. ornaments) that function as badges of status (Senar, 1999). Hence, there is a necessity to assess the physiological costs of being dominant in order to have a more balanced view of the factors involved in the establishment and evolution of dominance.

Oxidative stress refers to the detrimental accumulation of oxidative damage in cells and tissues, an accumulation primarily caused by an imbalance between the rate of reactive oxygen species (ROS) generation and the organism's antioxidant capacity (Finkel & Holbrook, 2000; Pamplona & Costantini, 2011). ROS are inevitable by-products of normal aerobic metabolism (Murphy, 2009). These highly reactive molecules play an important role in cell signalling by triggering multiple cascades of events favouring the maintenance of cellular functions (Nemoto, Takeda, Yu, Ferrans, & Finkel, 2000). However, when not sustained by the components of the antioxidant machinery (reviewed in Monaghan, Metcalfe, & Torres, 2009), excessive intracellular ROS have deleterious oxidizing effects on key biological molecules and are ultimately associated with the aetiology of numerous pathologies and the acceleration of senescence (Finkel & Holbrook, 2000; Monaghan et al., 2009). Such disequilibrium between ROS generation overpowering antioxidant defences has been proposed as a physiological mechanism underlying life history trade-offs (Monaghan et al., 2009; Selman, Blount, Nussey, & Speakman, 2012; Speakman et al., 2015). Although the link between energy expenditure and ROS production is still debated (see Salin et al., 2015; Speakman et al., 2015), oxidative damage is thought to be associated with (1) the overall metabolic activity, which generates ROS as a by-product (Murphy, 2009) and (2) the allocation of resources to crucial body functions such as growth and reproduction at the expense of antioxidant defences (Zhang & Hood, 2016).

Dominant individuals may face physiological challenges arising from high stress levels as evidenced by elevated circulating glucocorticoid levels (Creel, 2001) and neutrophils to lymphocytes ratios (Cohas et al., 2018). Dominants are also likely to exhibit high levels of sex hormones, such as testosterone, which is linked to aggressive behaviour (Archawaranon & Wiley, 1988; Wingfield, Ball, Dufty, Hegner, & Ramenofsky, 1987). Since stress and male sex hormones are modulators of oxidative balance and associated with oxidative stress (Alonso-Alvarez, Bertrand, Faivre, Chastel, & Sorci, 2007; Costantini, Marasco, & Møller, 2011) we can expect more aggressive or dominant individuals to be more susceptible to oxidative stress. Studies of the relationship between dominance status and oxidative status are still scarce; however, there is cumulative support in the literature for a close relationship between social rank and oxidative status. While some studies found a positive relationship between attaining a higher social rank and high oxidative stress (Beaulieu, Mboumba, Willaume, Kappeler, & Charpentier, 2014; Cram, Blount, & Young, 2015a; Van de Crommenacker, Komdeur, Burke, & Richardson, 2011), others found counterexamples in which high levels of aggressiveness and/or dominance are associated with lower levels of oxidative damage (e.g. Georgiev, Muehlenbein, Prall, Emery Thompson, & Maestripieri, 2015; Isaksson et al., 2011). This discrepancy between studies underlies the fact that the relationship between dominance and oxidative stress may be taxon specific (e.g. primates: Georgiev, et al., 2015; birds: Van de Crommenacker, et al., 2011; lizards: Isaksson et al., 2011), sex specific (Cram et al., 2015a) and context specific. For instance, the social structure (e.g. cooperative breeding system, Van de Crommenacker et al., 2011), the social stability (Beaulieu et al., 2014) or the season and reproductive state (Beaulieu et al., 2014; Cram et al., 2015a) at the time of the study are likely to have an impact on this relationship. More importantly, there is a discrepancy in the criteria used to determine dominance, which is determined either by considering the individual agonistic dominance (Beaulieu et al., 2014) or the breeding dominance (Cram et al., 2015a). Hence, more studies are needed to improve our understanding of this topic by adding evidence to disentangle the patterns that may occur amid this heterogeneity.

Here, we investigated whether there is a physiological cost, measured as oxidative stress, associated with individual dominance rank in a highly social, colonial and cooperatively breeding species of bird, the sociable weaver, *Philetairus socius*. These birds live in colonies structured by strongly ordered and stable hierarchies, with males being dominant over females (Rat, van Dijk, Covas, & Doutrelant, 2015). Dominance hierarchies are influenced by individuals' aggressiveness, and are signalled by a melanin-based bib, which is present in both sexes and possibly functions as a badge of status (Rat et al., 2015). Additionally, dominant individuals were found to obtain privileged access to food and reproduction (Rat, 2015).

Therefore, we expected that individual variation in oxidative status would be linked to social rank. To investigate this link, we assessed an individual's dominance status by scoring interactions over a food resource and tested whether dominance is related to oxidative status. Because measuring only one side of the oxidative balance could lead to misinterpretation (Monaghan et al., 2009), we assessed individual oxidative status by both oxidative damage and the antioxidant capacity (Costantini & Verhulst, 2009). If dominance is costly, we expected higher values of oxidative stress in higher-ranking individuals, characterized by higher oxidative damage and/or weaker antioxidant protection. However, subordinates may also be expected to incur higher physiological costs, for example, associated with received aggression and poor nutrition. Hence, subordinates may also experience high oxidative stress levels. Furthermore, we expected sex-specific differences in oxidative status as a result of sex-related differences in dominance status and the different reproductive strategies pursued by males and females (Costantini, 2017; Ellison, 2003; Monaghan et al., 2009).