



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.

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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).

Moreover, to disentangle the possible confounding effect of reproduction, we also assessed the relationship of dominance to previous and future breeding status. Finally, to better understand the link between dominance status and individual oxidative status, we examined whether this link can be affected by social stability by assessing the transitivity and consistency of dominance relationships.

METHODS

Study Species and Field Site

The sociable weaver is a colonial and facultative cooperatively breeding passerine that inhabits the semiarid savannahs of the southern Kalahari and Namib regions of Namibia and of South Africa's Northern Cape Province. This weaver species lives in large colonial nests, used for both roosting and breeding (Maclean, 1973). These structures are built cooperatively using mainly *Stipagrostis* grasses and are assembled on a variety of sturdy structures, with acacia trees being the most common. Sociable weavers inhabit a highly fluctuating environment characterized by an unpredictable rainfall, both in timing and in quantity. Rainfall is the main determinant of food availability through its effects on the abundance of seeds and insects on which these weavers feed (Maclean, 1973) and, consequently, determines breeding activity and success (Covas, Du Plessis, & Doutrelant, 2008). Sociable weavers may breed in pairs or cooperative groups with one to five helpers (Covas et al., 2008). As in most cooperative systems (e.g. Lardy, Allainé, Bonenfant, & Cohas, 2015; Nelson-Flower et al., 2011), sociable weavers' access to reproduction is skewed and associated with dominance (Rat, 2015) and age (Covas, Dalecky, Caizergues, & Doutrelant, 2006). Helpers are usually younger birds that postpone reproduction in the first years of life and help the parents raise their siblings.

Field work was conducted before the onset of the breeding season, from August to early September 2015, at Benfontein Game Farm (28°52'S, 24°50'E) near Kimberley (Northern Cape Province, South Africa), an area of open savannah encompassing ca. 25 sociable weaver colonies varying in size (ca. 10–130 individuals). This investigation was part of a long-term research project on the cooperative behaviour and population dynamics of this species. To this end, 13 colonies are captured annually at the study site using mist nets, which are placed around the colonies before dawn. When captured, all individuals are ringed with both a numbered metal ring and a unique colour combination, allowing for individual identification at recapture and from video recordings. During captures, blood samples are taken to genetically determine sex, parentage and relatedness (Griffiths, Double, Orr, & Dawson, 1998). Sex is determined by amplification of chromo-helicase-DNA-binding genes located on the W and Z sex chromosomes using the P2 and P8 universal primers (Griffiths et al., 1998). All individuals are weighed (to the nearest 0.01 g), and wing and tarsus length measured (to the nearest 0.5 and 0.01 mm, respectively). For this study, five colonies were captured, and colony size was estimated by counting birds caught and by adding the number of birds that were seen escaping by avoiding the nets (capture success is 85–100%, Covas, n.d.).

These captures, as well as regular visits to the nests during the breeding season to ring the nestlings, allow us either to accurately assess the age of the individuals marked as nestlings or to estimate a minimum age of individuals captured for the first time as adults.

Dominance and Behaviour Analysis

Dominance hierarchies were determined within five colonies using an already established protocol (Rat et al., 2015; Fig. 1) based



Figure 1. Sociable weavers aggressively interacting at an artificial feeding source in the field. This experimental set-up allows us to determine dominance hierarchies and assess the respective individual dominance rank among colony members.

on the behavioural analysis and scoring of agonistic interactions between individuals when feeding at an artificial food source (a mixture of bird seeds fed ad libitum) in a plate placed underneath each colony. Behavioural observations were performed using a video camera (Sony Handycam HD) on a tripod 2–3 m from the feeder, allowing us to record all interactions up to 1 m around the feeder. We conducted 2 h of observations every day, for 11.6 ± 0.730 (mean \pm SD) days per colony, with the recording process starting on 28 August 2015. These observations were done between 0900 and 1000 hours and repeated in the afternoon between 1400 and 1500 hours, for a total of 213 h each colony with a total of 42.6 ± 2.7 h (mean \pm SD) during the activity period of the birds at this time of year. The feeder was removed between recordings to increase competition and thus the number of interactions observed (Rat et al., 2015).

Both the type and direction of agonistic interactions observed were scored (as aggressions, displacements, threats and avoidances, see Table 1 for a summarized description). For each interaction the identity of the birds was also scored to assess the 'winner' and the 'loser'. In this species, the initiator is always the one determining the encounter outcome and considered as the winner in all types of interactions, except for avoidance, which was the opposite (the individual that avoided another was considered as the loser). To define a bird as resident at the colony, and to include possible immigrants and avoid prospecting birds (i.e. individuals that do not roost at the colony), we used the following criteria for colony attribution. A bird was considered as resident at the colony if it was captured at that colony or, when not captured, if

Table 1

Description of scored agonistic interactions at the feeder used to calculate individual David's scores

Type of agonistic interaction	Description
Aggression	Individual A physically attacks individual B by pecking, kicking or wing flapping
Displacement	Individual A moves directly towards a point of intersection with individual B until B moves away. Also includes chasing
Threat	Individual A intimidates individual B, raising the beak, fluffing out the head feathers and adopting a conspicuous position until B moves away, without involving physical contact
Avoidance	Individual B moves away from individual A, evading A without A moving directly towards to B

it appeared on at least 3 consecutive days at that colony. For individuals captured in more than one colony ($N = 3$) or that were recorded over more than 3 days in more than one colony, the colony attributed was the one in which they appeared for more days.

A total of 17 814 agonistic interactions were recorded in the five studied colonies (3568 ± 1427 (mean \pm SD) interactions per colony), from which dominance scores were calculated and obtained for 167 adult individuals (64 females, 90 males and 13 with unknown sex). These interactions were as follows: 4045 acts of aggression, 6739 displacements, 1463 threats and 5567 avoidances. Using the direction of the interactions, David's score (David, 1987) was used to determine each individual dominance score (for each colony). David's score appears to be the most appropriate method to assess individual rank, through overall individual success, since it is based on the unweighted and weighted sum of an individual's proportion of wins by taking the relative strength of the individual's opponent into account (Gammell, de Vries, Jennings, Carlin, & Hayden, 2003). This score is then calculated by the weighted sum of the individual's proportion of wins (weighted by the wins of the adversaries) minus the weighted proportion of losses (weighted by the losses of the adversaries), using the 'steepness' R package (De Vries, Stevens, & Vervaecke, 2006). Following Gammell et al.'s (2003) procedures, social dominance scores were standardized using: $\frac{DS_i - DS_{\min}}{DS_{\max} - DS_{\min}}$; here i represents the individual's score within the colony, and DS_{\min} and DS_{\max} the lowest and highest scores obtained in that colony. The final values ranged from 0 to 1 (from the most subordinate to the most dominant individual) and allowed us to compare scores between colonies of different sizes.

Oxidative Stress Assays

A blood sample (ca. 75 μ l) was taken from the brachial vein of each bird using a sterile needle and a heparinized capillary tube. The time of sampling in the day, as a proxy between capture and the completion of blood sampling and almost immediate release, was recorded. Blood samples were centrifuged in the field immediately after sampling at 2000 g for 2 min (Sprout minicentrifuge, Fisher Scientific, Loughborough, U.K.) and placed in a cooler box until frozen; they were stored and kept frozen at -20 °C at the field station for up to 6 h after sampling. The plasma was then shipped back to Europe in a Sofribox cool box (which keeps samples at -20 °C for up to 72 h) and stored at -80 °C until further analysis.

Each individual's oxidative profile was assessed by measuring concomitantly the (1) circulating oxidative damage measured by the amount of reactive oxygen metabolites (ROMs) and (2) nonspecific antioxidant capacity of plasma (OXY), two widely used markers in ecological studies (Costantini, 2016; Costantini, Cardinale, & Carere, 2007). Both components were quantified using commercial determination kits, the d-ROM and OXY-adsorbent tests, respectively (Diacron International, Grosseto, Italy), following the protocols developed by Costantini and Dell'Omo (2006).

Intra-assay (within-plate) repeatability for the ROMs and OXY levels was assessed by intraclass correlation coefficients; this method relies on the use of mixed-effects models to extract the partition of the variance's components and is calculated in the R package 'rptR' (Nakagawa & Schielzeth, 2010). The intra-assay repeatability for ROMs ($N = 722$) and OXY levels ($N = 924$) was 0.920 ± 0.008 SE and 0.905 ± 0.008 SE, respectively.

Breeding Status Assessment

The effect of dominance on oxidative status may be confounded by reproductive status (i.e. as a result of reproductive effort or preparation for future reproduction). Moreover, previous studies

have shown that (1) dominant individuals benefit from higher access to reproduction (Ang & Manica, 2010; Clutton-Brock et al., 2006; Monnin & Peeters, 1999) and (2) oxidative stress is a known proximate cost of reproduction (Alonso-Alvarez et al., 2004; Cram, Blount, & Young, 2015b; reviewed by ; Monaghan et al., 2009). For this reason, we tested whether individual dominance rank was related to previous and future reproduction by assessing the previous and future individual breeding status.

We monitored breeding activity by inspecting all nest chambers in the study colonies, every 3 days, during two breeding seasons (2014–2015 and 2015–2016). Reproductive status (breeder versus nonbreeder) was determined by a combination of genetic (Paquet, Doutrelant, Hatchwell, Spottiswoode, & Covas, 2015) and video analysis. Nests were recorded during incubation (only the breeding pair incubates the eggs) and nestling periods. During incubation, we recorded a minimum of 2 h in 2015–2016 only. During the nestling period we recorded the chicks between 4 and 20 days old, on at least 2 different days, for at least 2 h per recording (the chicks are fed by the parents and helpers).

We successfully identified the breeding pairs in 80% of all breeding attempts (90 of 112 breeding attempts) in 2014–2015 and 92% in 2015–2016 (63 of 68 breeding attempts). However, due to the high predation rate, many breeding attempts failed before we had the chance to record the nests; nevertheless a large proportion of these unidentified nests were likely to be occupied by already known pairs.

Statistical Analysis

To test whether individual oxidative status was predicted by individual dominance rank, two separate linear mixed models (LMMs) were performed with the levels of ROMs and OXY as dependent variables and dominance score as the main effect. Since other confounding variables could influence individual oxidative status we also included the following: sex; minimum age in years (range 1–8 years); time of sampling (0756–1141 hours), which was used as a proxy of the time elapsed between capture and the completion of blood sampling, as in the exploratory analysis this was found to have a highly significant effect on both markers ($P < 0.019$); colony size, as this has been reported to have an effect on oxidative status in other species (e.g. Cram et al., 2015b; Lardy, Rey, Salin, Voituron, & Cohas, 2016) and there may be stronger competition in larger groups; body mass (23.45–30.07 g) and tarsus length (22.24–24.68 mm) as measures of body condition. Body condition was also assessed through the residuals of the regression mass–tarsus length and showed similar results when we replaced tarsus length with mass. The most biologically relevant interaction terms were tested: dominance*sex, dominance*age and dominance*sex*age. We also investigated a possible quadratic relation between dominance and the markers by including both linear and quadratic components for each marker in the model, which was not significant. Colony identity was used as a random effect in all models to account for a possible correlation between behaviour and physiology within colonies and avoid pseudoreplication.

To assess the relationship between dominance status and breeding status in our population, we tested whether individual dominance rank was related to previous and future reproduction. We tested whether previous breeding status was related to dominance using an LMM with dominance score as the dependent variable, breeding status (breeder versus nonbreeder) during the breeding season from October 2014 to January 2015, sex, age and the interaction breeding status*sex as independent variables, and colony identity as a random effect. To test whether near future breeding status was related to dominance we did a similar analysis,

but individuals were defined as breeders if they were seen reproducing during the breeding season from October 2015 until January 2016.

To avoid potential multicollinearity problems, Spearman rank correlations for non-normally distributed variables and Pearson correlation for normally distributed variables were used to test possible correlations between the explanatory variables in each model (dominance score, sex, minimum age, tarsus, mass, breeding status). Only two sets of variables were found to be strongly correlated: sex with dominance score and age with breeding status ($r > 0.62$, $N = 154$, $P < 0.01$; for the remainder: $r < 0.46$). To assess the importance of these correlations through variance inflation of our models and avoid a possible distortion of the results, the variance inflation factor (VIF) was calculated using the 'AED' R package (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). As recommended by the authors, all VIF values were < 1.7 and, therefore, the models would not be affected by multicollinearity; we thus included the confounding factors sex and dominance for the oxidative stress analysis and breeding status and age for the breeding status analysis.

For the four models, a linear mixed-model approach was performed using the R package 'lme4' (Bates, Maechler, Bolker, & Walker, 2014). To verify the normality assumptions of linear mixed models, residuals were analysed using QQ plots, fitted versus residuals plots and histograms. To obtain a final model for the tests, we started with a full model with all variables including non-quadratic and quadratic terms. Then, using a backward stepwise approach, we successively removed nonsignificant explanatory variables based on the largest P values until only significant predictors remained ($P < 0.05$), starting with the interactions with the least significant values, to obtain a minimal model. All predictors were centred and standardized to a mean of 0 and an SD of 1, so that all estimates are comparable and to allow interpretation of single terms even in the presence of interactions, following the procedures described by Schielzeth (2010).

Finally, we tested whether the impact of dominance status on individual oxidative status varies as a function of social stability and rank maintenance (Sapolsky, 2005). To assess transitivity and consistency in dominance relationships for the five colonies included in this study we followed the same procedures as Rat et al. (2015). This allowed us to calculate the orderliness index (t_{tri}) using a social network-based technique, the triangle transitivity (i.e. if individual A is dominant over all others, individual B is dominant over all others but A, and so on to the last individual which is subordinate to all others, such as $A > B > C$; Shizuka & McDonald, 2012). We also performed this analysis for each sex separately, considering only male–male and female–female interactions, to assess possible differences in hierarchy structure between the sexes. Orderliness indices between 0 and 0.5 reflect egalitarian and unstable systems, 0.5 to 0.8 moderate hierarchies and 0.8 to 1 strongly ordered hierarchies characteristic of stable despotic systems (Bergstrom & Fedigan, 2010).

All analyses were conducted using R v. 3.2.5 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>).

Ethical Note

All experiments followed the ASAB/ABS guidelines for the Use of Animals in Research (ASAB/ABS, 2018) and were conducted with permission from the Northern Cape Department of Tourism, Environment and Conservation (permit FAUNA 1638/2015) and the approval of the Ethics Committee of the University of Cape Town (2014/V2/RC). Blood samples were taken under authorization of the South African Veterinary Council (AL17/15893 to R.C.).

Our procedures involved the capture, confinement, handling and blood sampling of the birds in the field, with the time elapsed between extracting the birds from the nets until the last bird was released ranging from 2 to 3 h. While queuing to be processed, birds rested in individual bird bags and were placed in a quiet, ventilated and shaded area. The sampling volume (ca. 75 μl) remained well below the prescribed limits for the percentage of total blood volume of this passerine. After handling, the birds were allowed to recover for a few minutes before being released in small groups. Any birds that showed signs of fatigue or injury were taken to an indoor aviary to recover and were subsequently released. This happened for less than 1% of the birds handled.

To decrease handling times, captures were conducted with a team of 8–12 experienced ringers that were allocated specific tasks to streamline the procedures conducted. However, our data did show an effect of handling time on birds' oxidative status markers ($P < 0.019$).

We are confident that the use of supplementary food did not increase the severity or frequency of agonistic interactions between the studied individuals, as no individual was seen being injured at the feeder.

RESULTS

Effect of Dominance on Plasma Oxidative Damage

Levels of ROMs increased significantly with individual dominance score in females, but not in males (significant interaction between dominance and sex; Table 2, Fig. 2). Age had a significantly positive effect, independently of sex or dominance rank (Table 2, Fig. 3). Body condition had no effect: there was a positive effect of tarsus length, but not of mass (Table 2). Colony size and the interactions between age and sex, dominance score and age, as well as the triple interaction between dominance score, age and sex, had no significant effect either (Table 2). The time elapsed between capture and blood sampling was positively related to levels of ROMs (Table 2, Fig. 4a).

Effect of Dominance on Plasma Antioxidant Capacity

Levels of OXY differed between the sexes, independently of rank, with males showing higher values than females (Table 2, Fig. 5). As with ROMs, time of sampling was also positively related to OXY levels (Table 2, Fig. 4b). Dominance, age, colony size and body condition had no effect on OXY levels (Table 2).

Dominance and Reproductive Status

Dominance was related to breeding status in males, but not in females, with dominant males showing a higher probability of being breeders in previous and future reproductive seasons (significant interactions between breeding status and sex for previous reproduction: Table 3, Fig. 6a; for future reproduction: Table 3, Fig. 6b). Dominance rank was also predicted by age, with a significant positive effect on individual dominance rank in the future reproductive season (Table 3), as well as a marginal effect on dominance in the previous reproductive season (Table 3).

Hierarchy Structure

We obtained an index of orderliness varying from 0.83 to 0.89 when considering all agonistic interactions. When testing for separate sexes and considering only male–male or female–female interactions, the orderliness indexes obtained were very similar (males: $t_{\text{tri}} = 0.843 \pm 0.028$ SE, $P < 0.05$; females:

Table 2

Results from two separate linear mixed models examining the effect of an individual's social dominance on oxidative status components for the sociable weaver

	ROMs				OXY			
	Estimate \pm SE	df	F	P	Estimate \pm SE	df	F	P
Intercept	-0.466 \pm 0.246				-0.294 \pm 0.180			
Dominance score (DSs)	1.721 \pm 0.746	104.036	1.188	0.278	-0.166 \pm 0.458	104.42	0.132	0.717
Age	0.214 \pm 0.421	104.142	4.62	0.034	0.041 \pm 0.092	103.75	0.194	0.66
Sex (male)	0.900 \pm 0.097	103.77	4.564	0.035	0.394 \pm 0.18	101.5	4.805	0.031
Mass	- 0.010 \pm 0.01	91.908	1.002	0.319	-0.006 \pm 0.108	104.941	0.003	0.953
Tarsus	0.241 \pm 0.01	103.787	6.029	0.016	0.011 \pm 0.103	103.564	0.011	0.918
Colony size	-0.067 \pm 0.102	14.376	0.431	0.522	0.207 \pm 0.111	11.754	3.496	0.087
Sampling time	0.226 \pm 0.01	99.246	5.634	0.019	0.258 \pm 0.094	104.63	8.121	0.005
Sex (male)* Age	0.117 \pm 0.196	103.021	0.356	0.552	0.228 \pm 0.297	103.474	0.589	0.445
DSs* Sex (male)	- 2.421 \pm 0.924	104.549	6.863	0.01	1.382 \pm 0.955	104.77	2.095	0.15
DSs* Age	-0.253 \pm 0.325	103.253	0.607	0.438	-0.198 \pm 0.328	102.81	0.364	0.548
DSs* Sex (male)* Age	1.539 \pm 1.235	104.123	1.552	0.216	-0.465 \pm 1.267	102.857	0.135	0.714

Reactive oxygen metabolites (ROMs) and nonspecific antioxidant capacity (OXY) were obtained for 105 individuals (61 males and 44 females). Estimates and *P* values are presented for all terms included in the exploratory model, with the terms included in the minimal model obtained in bold.

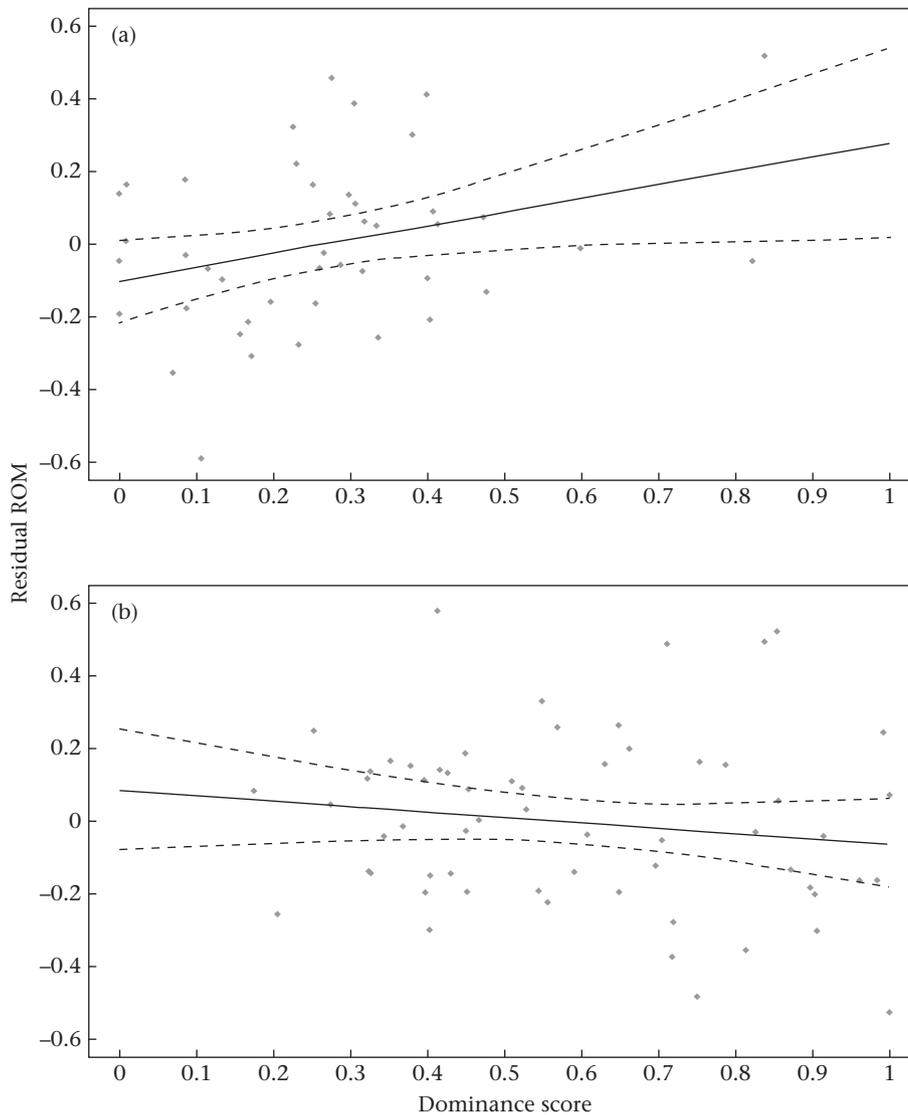


Figure 2. Relationship between the standardized David's score (individual dominance score) and the amount of reactive oxygen metabolites (ROMs) in (a) females ($N = 44$) and (b) males ($N = 61$) sociable weavers. Dots represent the observed data points, solid lines represent the model predictions and dashed lines show the associated standard errors. The residual values of ROMs were obtained after correcting for age, sex, mass, tarsus length and sampling time.

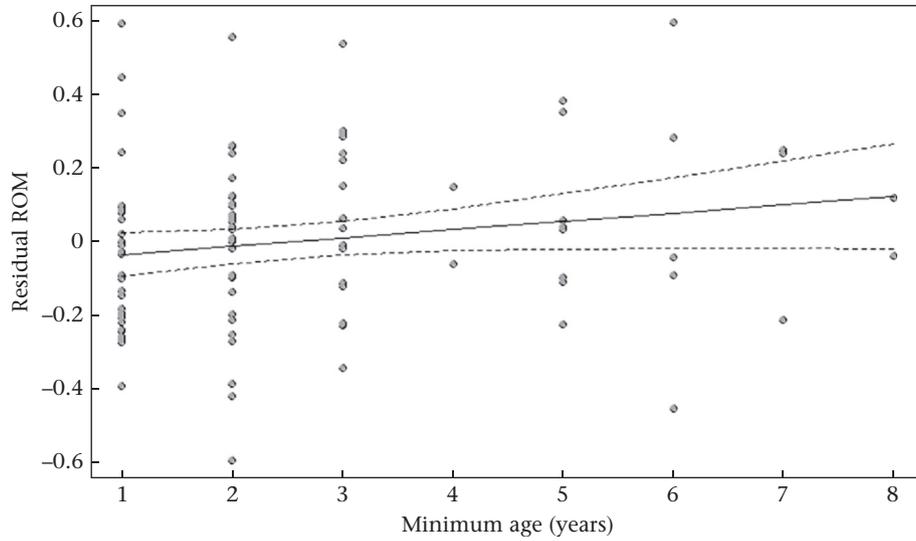


Figure 3. Relationship between minimum age in years and the amount of reactive oxygen metabolites (ROMs) for a total of 105 individuals (61 males and 44 females). Dots represent the observed data points, solid lines represent the model predictions and dashed lines show the associated standard errors. The residual values of ROMs were obtained after correcting for dominance score, sex, mass, tarsus length and sampling time.

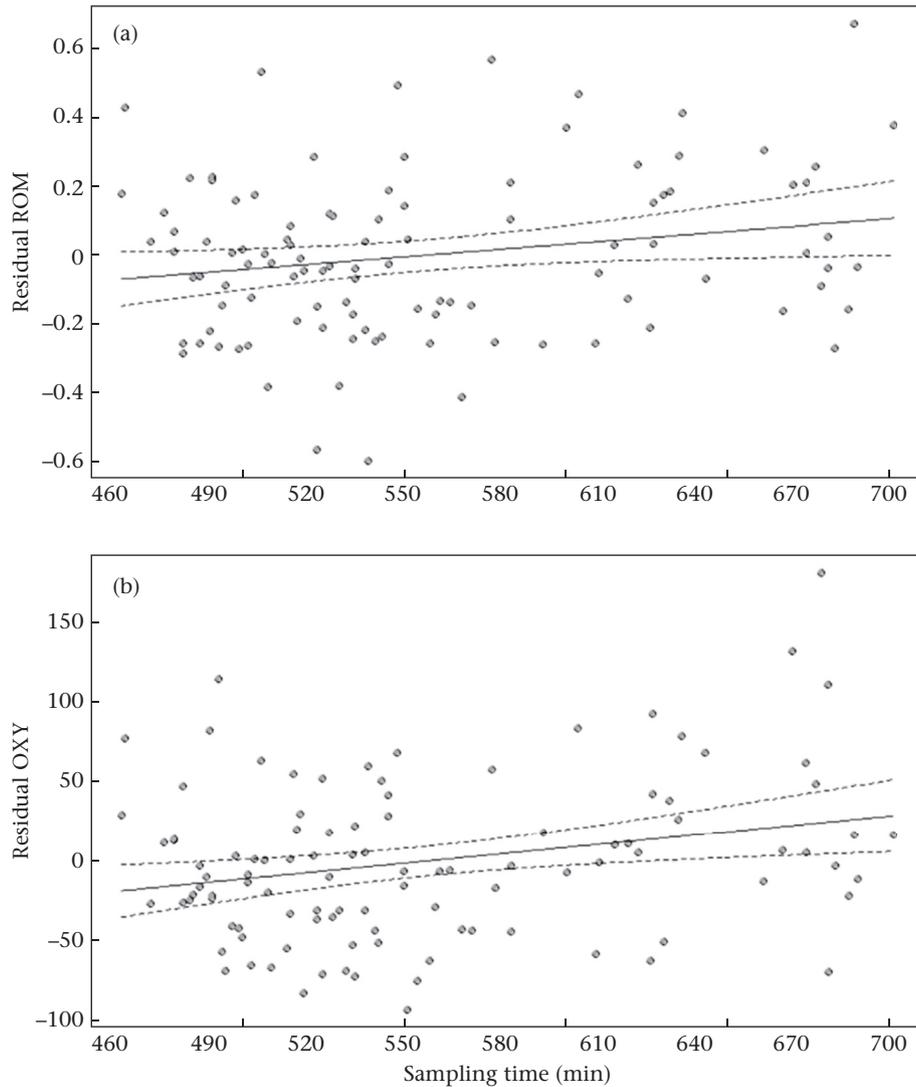


Figure 4. Relationship between sampling time (min) and (a) the amount of reactive oxygen metabolites (ROMs) and (b) the nonspecific antioxidant capacity (OXY) for a total of 105 individuals (61 males and 44 females). Dots represent the observed data points, solid lines represent the model predictions and dashed lines show the associated standard errors. The residual values of ROMs were obtained after correcting for dominance score, age, sex, mass and tarsus length. The residual values of OXY were obtained after correcting for sex.

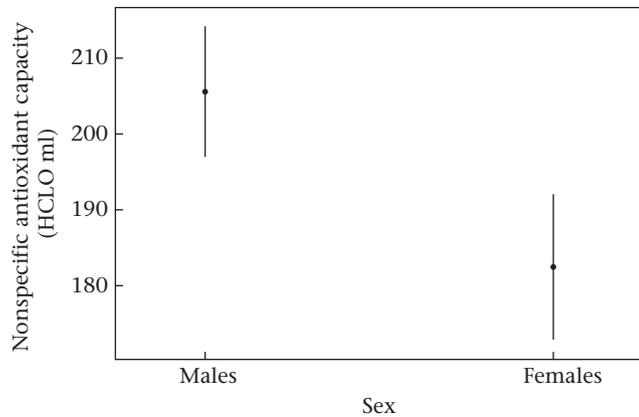


Figure 5. Relationship between sex and the nonspecific antioxidant capacity (OXY) (model estimates \pm SE, Table 2) for a total of 105 individuals (44 females and 61 males).

$t_{\text{tri}}=0.88 \pm 0.023$ SE, $P < 0.47$) Nevertheless, the index was not significant for one of the colonies when considering all individuals and for three of the colonies when only considering same-sex interactions ($P > 0.073$). This is probably due to the high frequency of unknown dyads.

DISCUSSION

In the present study, we investigated the possible physiological costs underlying social dominance in sociable weavers. Our results suggest that oxidative stress underpins a possible trade-off between the benefits of dominance and the associated physiological costs. However, this effect appears to occur only in females. Our results also indicate that plasma oxidative damage increases with age, regardless of dominance status or sex. Finally, we found a significant effect of the time elapsed since capture on the two oxidative stress markers.

The positive relationship between ROMs and dominance in females may be related to the increase in aggressive and policing behaviour with rank (e.g. displacements and threatening), which are characteristic of both dominance acquisition and maintenance. We believe that this effect is a direct consequence of dominance rank and not a confounding effect of reproduction as could be expected for dominant individuals (as a result of reproductive effort or the preparation for future reproduction; Monaghan et al., 2009). Indeed, we found that breeding status during previous and future reproductive periods was independent of the current dominance rank in females of this species. Although sociable weaver females are less often engaged in aggressive interactions than males (only 13% of all aggressive interactions were initiated by females versus

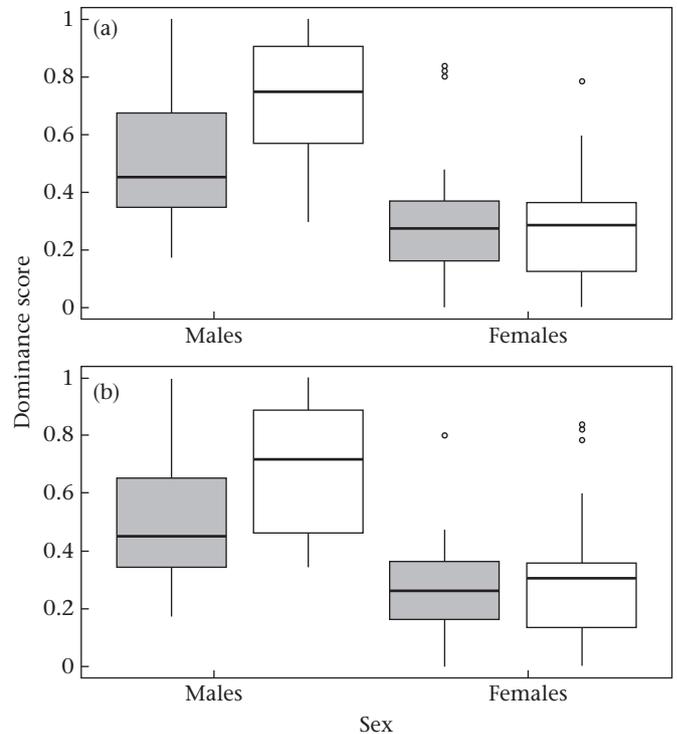


Figure 6. Relationship between dominance score and breeding status from (a) previous reproduction (season 2014–2015) and (b) future reproduction (season 2015–2016) for males and females (model estimates \pm SE, Table 3). From the total of 154 individuals seen interacting at the feeder (90 males and 64 females), 54 individuals were identified as breeders (30 males and 24 females) against 59 individuals (34 males and 25 females), from previous and future reproductive seasons, respectively. Distance between nonbreeders (grey bars) and breeders (white bars) represents variation in dominance. The box plots show medians (horizontal lines) and interquartile ranges (boxes). Whiskers show the spread of data (highest and lowest values within 1.5 interquartile ranges). Open circles are outliers.

87% initiated by males), fights combined with other behaviours required to reach and maintain a higher rank in females may represent a cost high enough to cause an overproduction of ROS. For example, in male territorial albino mice, *Mus musculus*, aggressiveness was strongly linked to the generation of ROS in peripheral granulocytes, and, thus, to an altered oxidative status (Rammal, Bouayed, & Soulimani, 2010). Furthermore, and in agreement with previous findings by Rat et al. (2015), the sociable weaver dominance hierarchy is strongly linear, as is characteristic of a despotic and stable society. In some despotic societies, dominant individuals continually and aggressively reassert their dominance rank over their subordinates (even when not challenged), resulting in a continual rank maintenance through physically

Table 3
Results from two separate linear mixed models examining the relationship between an individual's social dominance and previous and future breeding status for the sociable weaver

	Previous reproduction				Future reproduction			
	Estimate \pm SE	df	F	P	Estimate \pm SE	df	F	P
Intercept	0.308 \pm 0.033				0.272 \pm 0.318			
Breeding status (breeder)	-0.067 \pm 0.056	154	1.216	0.272	0.033 \pm 0.05	154	8.684	0.004
Sex (male)	0.214 \pm 0.040	154	91.374	<0.001	0.241 \pm 0.041	153.29	85.654	<0.001
Age	0.036 \pm 0.02	154	3.189	0.076	0.048 \pm 0.016	153.35	8.762	0.004
Breeding status (breeder)*Sex (male)	0.227 \pm 0.07	154	11.19	0.001	0.131 \pm 0.067	154	3.989	0.047

Breeding status was assessed from two seasons: 2014–2015 (i.e. previous reproduction) and 2015–2016 (i.e. future reproduction), for the total of 154 individuals seen interacting at the feeder (90 males and 64 females). Estimates and P values are presented for all terms included in the exploratory model, with the terms included in the minimal model obtained in bold.

demanding fights, and with dominant individuals suffering the greatest physiological costs (Sapolsky, 2005). There is no clear evidence of a direct link between energetic demands and ROS production (Speakman et al., 2015); nevertheless there is accumulating evidence that energetically demanding activities such as flight, reproductive effort and aggressive behaviours can lead to high accumulation of ROMs in plasma (Colominas-Ciuró, Santos, Coria, & Barbosa, 2017; Costantini, Dell'Arciccia, & Lipp, 2008; Rammal et al., 2010). Although the hypothesis of an increase in ROS with increased aggression cannot be directly validated in our study, the increase in level of ROMs with rank indicates that female sociable weavers struggle to maintain redox homeostasis when attaining and maintaining a higher and demanding dominant position.

Although a similar scenario could also be expected in dominant males, the lack of rank-related differences in males in the level of ROMs may be explained by the differential access to food resources, and, presumably, the differential intake of antioxidant dietary resources (Catoni, Peters, & Schaefer, 2008), experienced by the two sexes. In sociable weavers, females are generally subordinate to males (only 28% of females reach a medium or higher rank, i.e. showing a standardized dominance score equal or above 0.333, compared to almost 98% of males), and in a previous study had reduced access to an artificial food source (a plate placed under the colony, Rat, 2015). From a physiological point of view, this differential access to resources may lead to the observed sex-specific differences in total antioxidant capacity, with lower OXY levels found in females than in males. This sex difference in OXY levels and other antioxidant components has been repeatedly found in many species (Isaksson, 2013; Wegmann, Voegeli, & Richner, 2015; reviewed by ; Constantini, 2017) and suggests that the compensatory ability of the organism's antioxidant capacity to mitigate the dominance-related ROS production in females may be failing. This possible effect of access to food might have been stronger given the particularly dry season caused by the 2015 El Niño (South African Weather Service). Both physiological markers used here are likely to be influenced by food quantity/quality, since several dietary oxidants and antioxidants can be detected by the assays (Costantini, 2010; Costantini et al., 2006). Moreover, restricted dietary access may have prevented females from increasing their antioxidant protection, which is depleted after reproduction, to the normal basal levels outside the breeding season. Although we found no significant differences in body condition between the sexes, females may not have the same access to high-quality food as males and, simultaneously, may need more energy, nutrients and time to recover from the physiological cost of reproduction, possibly having negative consequences for their oxidative status. This hypothesis, nevertheless, remains to be tested.

Another nonexclusive explanation for the sex differences found here in redox physiology may result from the contrasting physiology and the reproductive strategies of each sex (Costantini, 2017; Ellison, 2003). Sex differences in resources allocated to reproduction, arising from egg production (e.g. carotenoids allocated to eggs, Blount, Houston, & Møller, 2000), and the energetics of incubation (Visser & Lessells, 2001), as well as the differential pattern of circulating hormones (Halliwell & Gutteridge, 2007), are likely to lead to a higher physiological cost of reproduction for females and may explain a higher oxidation risk (Alonso-Alvarez et al., 2004; Travers, Clinchy, Zanette, Boonstra, & Williams, 2010). For example, Cram et al. (2015a), found that in the white-browed sparrow weaver, *Plocepasser mahali*, both females and males showed a decline in antioxidant defences over the course of the breeding season. However, this decline remained minor in males and was marked in dominant females (the only females that lay and incubate eggs and are the main nestling providers). Sociable weavers have variable and usually long breeding periods (from 3

months to year-round breeding). Our study was conducted approximately 3 months after the end of the previous breeding period, which lasted 7 months. This time coincided with the end of winter, which is a dry and cold season and is thought to be particularly demanding energetically for females, as reflected by the positive effect of both temperature and rainfall on the onset of breeding (Mares, Doutrelant, Paquet, Spottiswoode, & Covas, 2017). Furthermore, our sampling was conducted during the beginning of 2015's strong El Niño event, which caused severe drought in this region. Hence, these harsh environmental constraints may have exacerbated the sex differences found in the relationship between dominance and oxidative status, with females still recovering from the breeding effort while facing a particularly dry winter.

Evidence is growing that susceptibility to oxidative stress plays an important role in shaping individual survival by functioning as a proximate physiological mechanism underlying individual life history trade-offs between self-maintenance and crucial life functions such as reproduction, growth and maintaining body condition (Alonso-Alvarez et al., 2004; Finkel & Holbrook, 2000; Monaghan et al., 2009; Selman et al., 2012). The differences found in antioxidant defences between the sexes in this study, and, thus, in the susceptibility to oxidative stress, could account for the covariation between major life traits and life span, in a sex-specific manner. Although we do not know whether there are sex differences in sociable weaver longevity, previous results suggest that reproduction has higher survival costs for females (particularly younger females) than for males (Paquet et al., 2015).

ROMs were also found to be positively related to age. Older sociable weavers seem to be more susceptible to environmental, social and/or physiological stressors than younger ones. This relationship has been found in several species (Martin & Grotewiel, 2006) and has been explained either by a higher rate of ROS production associated with mitochondria dysfunctions or by a higher intrinsic susceptibility of molecules to ROS as the result of the cellular processes related to ageing (reviewed in Monaghan et al., 2009). Older sociable weavers are also more likely to be breeding birds (the age of first breeding is rarely below 2 years of age; Covas, Doutrelant, & du Plessis, 2004). Hence the age effect detected here could, to some extent, also reflect the cost of reproduction, a possibility that would require further investigation.

The higher levels of OXY found in males, and which were not related to dominance, mass and/or tarsus length, can be related to an overall higher access to food, as discussed above. The fact that antioxidant defences were independent of rank and body condition in the sociable weaver appears to contradict the hypothesis that dominant individuals are in better condition due to intrinsic quality or better competitive ability. Similar results were found in male white-browed sparrow weavers (Cram et al., 2015a) and in male mandrills, *Mandrillus sphinx* (Beaulieu et al., 2014), where no differences in antioxidant capacity between dominant male breeders and subordinate male nonbreeders were detected. However, these intrinsic differences could be masked by other physiological and behavioural mechanisms associated with the different categories of individuals. Specifically, dominants may be better intrinsically and/or have better access to resources, but pay a higher cost arising from policing and aggression, while subordinates or lower quality individuals may avoid these costs. Hence, while our results showed that antioxidant defences were not related to status in our population, further experimental work is needed to address the underlying, causal factors.

Time of sampling (used as a proxy between capture and the completion of blood sampling) had a significant effect in determining the variation of both markers used in this study. This contrasts with previous studies which found no effect of acute increases in stress (handling or containment) on short-term

changes in ROMs or OXY levels (Costantini et al., 2007; Herborn, Coffey, Larcombe, Alexander, & Arnold, 2011, but see Cohen, Klasing, & Ricklefs, 2007 for stress-induced effects on other oxidative stress markers). Nevertheless, stress responses are known to lead to increases in corticosterone, which was found to be linked to an increase in both the production of ROS and a compensatory increase in antioxidant capacity in broiler chickens, *Gallus gallus domesticus* (Lin, Decuyper, & Buyse, 2004). Our results suggest that in studies conducted on wild populations, which require long periods of handling due to field work constraints, handling time should be considered when analysing and interpreting the results.

Here we used two independent measures to assess the oxidative status of sociable weavers, but previous studies on mammals indicated low or no correlation between different oxidative stress markers (Christensen et al., 2015). It is therefore recommended to use multiple markers for both components of the oxidative status, but this was not possible in our study due to the small amount of blood that we were able to obtain per individual (sociable weavers weigh ca. 27 g). Hence, care must be taken when generalizing from these results, as different oxidative stress markers may reflect different and potentially uncoupled biochemical processes in different tissues and different species (Christensen et al., 2015; Monaghan et al., 2009; Speakman et al., 2015).

To our knowledge, this is the first study to examine the link between oxidative status and an individual's position in the social hierarchy (i.e. dominance rank) in a wild species of bird. Previous studies have investigated the relationship between oxidative status and dominance measured as breeding status (Cram et al., 2015a; Van de Crommenacker et al., 2011). However, in these studies breeders were usually found to be dominant over nonbreeders, which makes it even harder to disentangle the costs of reproduction and social rank, and it ignores differences in dominance rank between nonbreeders; understanding these differences is required for a comprehensive understanding of the costs and benefits of sociality.

The findings from our study add to the cumulative evidence that dominance is underpinned by oxidative stress in different contexts. Measuring physiological components such as individual oxidative status therefore seems a useful tool to decipher the hidden physiological costs underlying dominance and the life history trade-offs associated with living in animal societies. Furthermore, we have shown that the relationship between dominance and oxidative stress is different for males and females. This has implications for understanding how sociality shapes females' health and survival patterns and opens a promising avenue for future research.

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