

SHORT COMMUNICATION

The oxidative cost of unstable social dominance

Michaël Beaulieu^{1,*}, Sylvère Mboumba², Eric Willaume³, Peter M. Kappeler⁴ and Marie J. E. Charpentier⁵**ABSTRACT**

High social rank is expected to incur fitness costs under unstable social conditions. A disruption of the oxidative balance may underlie such effects, but how markers of oxidative stress vary in relation to social rank and stability is unknown. We examined in mandrills whether the mating season characterized by social instability between males (but not between females) affected their oxidative balance differently according to their social rank. Outside the mating season, high-ranking males showed the lowest levels of oxidative damage, while during the mating season, they were the only males to experience increased oxidative damage. In contrast, the mating season increased oxidative stress in all females, irrespective of their social rank. These results support the hypothesis that the coupling between social rank and social stability is responsible for differential costs in terms of oxidative stress, which may explain inter-individual differences in susceptibility to socially induced health issues.

KEY WORDS: Dominance, Ecophysiology, Health, Mandrill, Oxidative balance, Social rank

INTRODUCTION

The relative position of an individual within its social environment considerably impacts on its health and fitness. Under certain circumstances, high-ranking individuals are healthier than subordinates, while under other conditions the opposite is true (Sapolsky, 2005). These context-dependent effects are likely to be due to the social stability of the group in which the individuals live. Under stable conditions, high-ranking individuals are favoured if they have enhanced access to resources that promote health (e.g. food, shelter, money), while under unstable conditions, these advantages may be counterbalanced by the costs related to the active establishment and maintenance of dominance (e.g. fights, injuries, time devoted to fight instead of feeding or medicating).

Because oxidative stress has been associated with both social stress and the occurrence of diseases in humans (Epel et al., 2004; Aruoma, 1998), it appears as a probable physiological mechanism underlying the effects of social environment on health. Oxidative stress, which results from the imbalance between the production of reactive oxygen species (ROS, a normal by-product of the aerobic metabolism) and antioxidant defences, can indeed disrupt physiological functions by inflicting damage on biological compounds. This suggests that oxidative stress may be caused by

social stress, which in turn may contribute to health issues. However, how the coupling of social rank and social stability may differently affect individuals in terms of oxidative stress remains unknown.

We examined this question in a seasonally breeding primate, the mandrill [*Mandrillus sphinx* (Linnaeus 1758)]. This species lives in hierarchically structured groups where social stability and instability co-occur. On the one hand, social rank in females is maternally inherited and stable, as females stay together within matrilineal groups throughout life. On the other hand, male social ranks are unstable because males regularly disperse from group to group. This social instability is exacerbated during the mating season when the number of males co-existing within female groups significantly increases (Abernethy et al., 2002). As a consequence, intra-sexual competition dramatically increases, with frequent changes in male hierarchy. Ferocious inter-male competition for reproduction is therefore likely to increase social stress for both males and females within the group. Based on the hypothesis that social stress increases oxidative stress, we postulated that the mating season would be associated with increased oxidative stress in mandrills. However, because of the social instability between males and the social stability between females, we expected these effects to be sex-biased, with highest effects in high-ranking males.

RESULTS

Overall, male mandrills exhibited slightly higher levels of oxidative damage during the mating season than outside it (23.9 ± 1.0 versus 22.9 ± 0.8 mg H_2O_2 dl^{-1} ; $F_{1,46}=9.27$, $P=0.01$). This was because, in high-ranking males, levels of oxidative damage were low outside the mating season and increased importantly during the mating season, while in low-ranking males, they were high and stable irrespective of the season (Fig. 1A). Such differences were reflected by a significant interaction between rank and season ($F_{2,45}=7.39$, $P=0.01$). As a result, outside the mating season, high-ranking males showed lower levels of oxidative damage than low-ranking males (least square differences: $P<0.03$), while during the mating season, they were the only ones to experience an increase in oxidative damage (least-square differences: $P<0.04$). We also found a significant interaction between age and season ($F_{2,45}=5.90$, $P=0.04$), with old males having lower levels of oxidative damage outside the mating season than during the mating season, while the season did not affect oxidative damage in young males (Fig. 2). No other variables had an effect on oxidative damage in males (all $P \geq 0.27$), and no variable had an effect on their antioxidant defences (all $P \geq 0.48$; supplementary material Table S1; Fig. 1B).

Season also had a strong effect on the oxidative balance of females: during the mating season, females experienced levels of oxidative damage 20% higher than outside the mating season (28.9 ± 1.4 versus 23.6 ± 1.0 mg H_2O_2 dl^{-1} ; $F_{2,42}=10.20$, $P=0.008$; Fig. 1C), while their antioxidant defences were 10% lower (291.1 ± 8.3 versus 322.0 ± 7.8 mmol^{-1} HOCl; $F_{1,43}=9.14$, $P=0.01$; Fig. 1D). No other variables had an effect on their oxidative markers (all $P \geq 0.17$; supplementary material Table S2).

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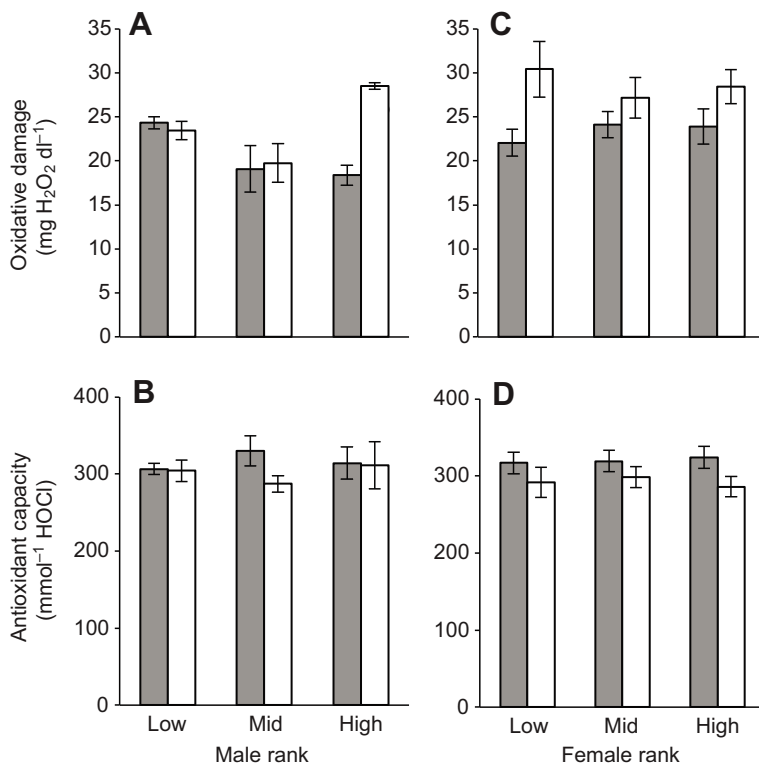


Fig. 1. Oxidative balance of male and female *Mandrillus sphinx*. Data are presented for male (A,B) and female (C,D) mandrills outside the mating season (grey bars) and during the mating season (white bars). Plasma oxidative damage is represented in A and C, while plasma antioxidant capacity is represented in B and D. Data are given as means \pm s.e.m.

DISCUSSION

During the mating season, social stress was expected to increase and to translate into higher levels of oxidative stress. Overall, our results support this hypothesis, as we found that the mating season was associated with higher levels of oxidative stress both in females and males than outside the mating season. Specifically, females exhibited lower antioxidant defences and higher oxidative damage, irrespective of their social rank. However, in males, this oxidative cost was only observed in high-ranking individuals, which exhibited higher levels of oxidative damage. This oxidative cost in high-ranking males is likely to be due to the social stress resulting from the effects of the maintenance of their social dominance through fights with other males to mate with females. These results are in

agreement with previous studies showing that inter-individual differences in aggressiveness can lead to variation in oxidative status (Isaksson et al., 2011). The high levels of oxidative damage in high-ranking males may also be exacerbated by their investment in secondary sexual signals. Indeed, high-ranking male mandrills develop spectacular coloured skin ornaments during the mating season (e.g. red face, mauve rump, red penis), while low-ranking male mandrills are arrested in their capacity to exhibit such physical features (Setchell and Dixon, 2001). Because the production of these secondary sexual signals is likely to increase oxidative stress, it may be hypothesized that they are honest signals of the capacity of males to combat oxidative stress if only males with high antioxidant defences can produce them. In contrast to this hypothesis, we did not find that high-ranking males increased their antioxidant defences during the mating season. However, we found that high-ranking males experienced lower levels of oxidative damage than low-ranking males outside the mating season. This suggests that high-ranking males had more room for increasing oxidative damage during the mating season than low-ranking males. Consequently, high-ranking males had the possibility to engage in aggressive social behaviours or express secondary sexual signals that may elevate oxidative damage during the mating season without experiencing excessive levels of oxidative damage, relative to other males. In contrast, such a strategy might expose low-ranking males with pre-existing high levels of oxidative damage to critical levels.

Inter-individual differences in terms of oxidative damage outside the mating season may be caused by age differences between males. Indeed, we also found that the age of males affected their levels of oxidative damage outside the mating season, while it did not affect levels during the mating season. In male mandrills, dominance rank increases with age from 6 to 11 years, remains stable between 11 and 16 years, and decreases afterwards (Setchell et al., 2006). This variation in social rank closely mirrors the variation in oxidative damage that we observed outside the mating season, as the decrease

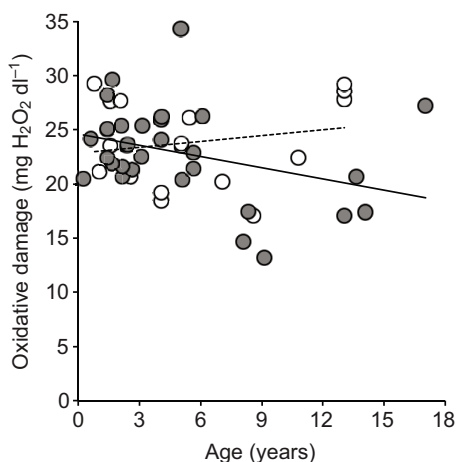


Fig. 2. Scatter plots showing the relationships between age and oxidative damage in male mandrills. The white dots and the dashed line correspond to the mating season, and the grey dots and the solid line correspond to the non-mating season.

in oxidative damage with age appears to be accentuated in males older than 6 years (with the notable exception of the one male in our study that had reached the advanced age of 16 years) (Fig. 2).

Testosterone regulates the expression of secondary sexual signals in male mandrills (Setchell et al., 2010). Yet, the secretion of testosterone has been described as decreasing when oxidative stress increases (Turner and Lysiak, 2008). High levels of oxidative stress outside the mating season may therefore participate in the arrested development of the secondary sexual signals of young low-ranking males during the following mating season, by inhibiting testosterone secretion. Consequently, levels of oxidative damage outside the mating season may be decisive for male mandrills, as they appear to have an important impact on their subsequent social rank during hierarchy establishment in the mating season, and thus on their chances to reproduce (Charpentier, 2005).

The variation in oxidative damage that we report here may reflect other physiological changes co-occurring during the mating season. Indeed, male mandrills that impose their dominance during the mating season have also been described as exhibiting increased levels of glucocorticoids (Setchell et al., 2010), which may significantly reduce their resistance to oxidative stress (Costantini et al., 2011). Accordingly, our results on oxidative damage closely mirror these variations in glucocorticoids, with high-ranking males experiencing lower levels of oxidative damage than subordinates under stable conditions, while the opposite is true under unstable conditions. Although levels of glucocorticoids reflect the stress currently experienced by individuals, oxidative markers may provide further information about the effects of such stress on health and fitness components (Aruoma, 1998). For instance, women under social stress exhibit shorter telomere length (a marker of ageing), which may be partly due to high oxidative stress (Epel et al., 2004). Under the hypothesis that mandrills can experience health issues induced by oxidative stress, low-ranking males would experience them throughout the year, while high-ranking male mandrills would experience them only during the mating season. Because high-ranking males have the highest reproductive success among male mandrills (Charpentier, 2005), our results suggest that, during the mating season, high-ranking males temporarily trade their oxidative balance and thus their health against the possibility of reproducing.

Our study revealed that social rank and social stability both affected oxidative status in a hierarchically structured species, and suggests that oxidative status before the mating season may participate in the establishment of social status during the mating season. However, because our study was conducted in a vulnerable species, we were constrained to conduct our measurements only on blood samples. Moreover, we considered only two markers of oxidative status. Consequently, our results may not give a full picture of the interplay between social rank, social stability and oxidative status. Therefore, further studies considering other biological matrices and markers of oxidative status would be needed to assess the generality of our findings.

MATERIALS AND METHODS

The study population of wild mandrills inhabits the Lékédi Park in Southern Gabon (Bakoumba). Since early 2012, behavioural data have been collected daily on individually recognized animals within the framework of the 'Mandrillus Project'. Using daily *ad libitum* records of aggressive and approach-avoidance behaviour between individuals in the study group (see Setchell and Dixon, 2001), we defined three social ranks in males: high-ranking (alpha and beta males), mid-ranking (males of ranks 3, 4 and 5, including adult and sub-adult males) and low-ranking (sub-adults and young

males of lower ranks) males. Similarly, we also defined three social ranks in females, high-, mid- and low-ranking, by following the same approach and by respecting the identities of matrilineal.

On three occasions (April 2012 and 2013, non-mating season; and September 2013, end of the mating season), we captured a subset of the study mandrills by blowpipe intramuscular injections of ketamine (Imalgene 1000; 7 mg kg⁻¹ for adults, 5 mg kg⁻¹ for juveniles) and xylazine (Rompun; 3 mg kg⁻¹ for adults, 5 mg kg⁻¹ for juveniles). We collected blood from the iliac vein of 66 individuals (1–3 samples per individual) with heparinized syringes. The time elapsed between capture and bleeding was consistent across individuals (about 10 min). After centrifugation of the blood samples, plasma was separated from erythrocytes and stored at -20°C. Plasma oxidative balance was then examined with (1) the d-ROM test (Diacron International, Grosseto, Italy), which measures the concentration of hydroperoxide, a reactive oxygen metabolite resulting from the attack of ROS on organic substrates (thereby reflecting oxidative damage), and (2) the OXY-adsorbent test (Diacron International), which measures total antioxidant capacity. Intra-assay coefficients of variation were 3% and 10%, respectively, and inter-assay coefficients of variation were both 8%.

To examine how oxidative markers vary between social ranks in relation to season, we fitted a general linear mixed model with rank, season and their interactions as fixed factors. Individual identity was coded as a random factor. As both social rank and oxidative markers may depend on the age of individuals (Setchell et al., 2006), we also controlled for this factor (and for its interactions with other variables) in our models. We knew the precise age of 17 individuals and estimated it for 49 others using body conditions, and dental eruption pattern in juveniles. The age range was between 0.25 and 17.03 years in males, and between 0.07 and 20.15 years in females. We used a descending procedure starting with all predictors and removing those with $P > 0.10$. As male and female social ranks are independent from each other, we conducted statistical analyses in males and females separately. Data were normally distributed and statistical analyses were performed using SAS version 9.4 (Proc GLIMMIX).

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Competing interests

The authors declare no competing financial interests.

Author contributions

M.J.E.C. and P.M.K. designed the study; M.J.E.C., S.M. and E.W. collected data in the field; M.B. performed laboratory analyses; and M.B. and M.J.E.C. wrote the article.

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Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.104851/-DC1>

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