

Original Article

Male quality, dominance rank, and mating success in free-ranging rhesus macaques

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In social mammals, condition and health are important determinants of the ability of males to achieve high dominance rank. Measures of individual condition are also predicted to affect male fitness via female preference for high-quality mates. We examined intermale variation in phenotypic quality (immune function and oxidative stress) in relation to male dominance status and mating success in a species with prominent female choice and a lack of male–female sexual coercion, the rhesus macaque (*Macaca mulatta*). We quantified immunity via 2 functional assays of innate immune response (bacteria killing assay and hemolytic complement assay) and measured oxidative stress via a lipid peroxidation assay in 15 adult males from 1 social group of macaques on Cayo Santiago, Puerto Rico. We then observed these males throughout the mating season to test the prediction that males in better condition achieved higher mating success. Males with more robust innate immune response and lower oxidative damage mated with a greater number of potentially fertile females. Male dominance rank, however, also correlated with our measures of quality. Higher-ranking males had more robust functional innate immune response and lower levels of oxidative damage. After accounting for rank, male quality was no longer correlated with mating success. These results demonstrate a potentially important role of male phenotypic quality in the mating system of a long-lived, group-living primate. What are the exact behavioral mechanisms via which sexual selection may operate on traits related to immunocompetence and resistance to oxidative damage in this species, however, remains an open question.

Key words: bacteria killing assay, ecoimmunology, hemolytic complement assay, innate immune function, oxidative stress, TBARS.

INTRODUCTION

For many male vertebrates, greater body size, armament size, strength, and/or superior fighting ability predict their ability to dominate other males (Andersson 1994; Berglund et al. 1996; Emlen 2008; Chelliah and Sukumar 2013). More dominant males gain fitness advantages by being more effective at monopolizing access to fertile females, by sexually coercing females, and/or by being more attractive to females as mating partners. Individual condition, or quality, therefore can affect not only male competitive ability in the context of intrasexual contests but also female mate choice (Andersson 1994, 2006; Andersson and Simmons 2006; Clutton-Brock and McAuliffe 2009). Male dominance, however, is not always related to quality. Differences in context and motivation may affect outcomes of agonistic interactions, independently from the quality of contestants (Qvarnström and Forsgren 1998).

Female preference for mating with highly competitive males may also vary in time and in space depending on the cost/benefit ratio of exhibiting such a preference (Wong and Candolin 2005), as well as in relation to the quality of the female (Holveck and Riebel 2010) and the intensity of female–female competition for mates (Fawcett and Johnstone 2003). Accordingly, female preference for males other than the most dominant, or higher-ranking, ones have been observed in a variety of taxa (Qvarnström and Forsgren 1998; Spence and Smith 2006; Polkki et al. 2012). What male traits females are choosing in such cases is often unclear.

Two aspects of male quality that might influence female mate choice are immunocompetence (Hamilton and Zuk 1982; Folstad and Karter 1992) and resistance to oxidative damage (Schantz et al. 1999). Males with higher immunocompetence—the ability to resist and cope with parasites and infections—are hypothesized to be able to exert greater reproductive effort without compromising their health and survival to the same extent as less immunocompetent males. Such males are expected to be more attractive to females, who should be able to recognize their quality from honest

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signals, or handicaps, such as sexual ornaments and/or behavioral displays (Jacobs and Zuk 2012). Meta-analyses of the literature show that male attractiveness is correlated, albeit weakly, with offspring immunocompetence and condition across taxa (Prokop et al. 2012), suggesting that female preference for more attractive males could increase female reproductive success. The existing evidence, however, is taxonomically restricted mainly to birds, insects, and fish: although the studies analyzed by Prokop et al. (2012) covered 55 different species, only one of those was a mammal, the bank vole, *Myodes glareolus* (Kruczek and Zatorska 2008).

Resistance to oxidative stress has also been suggested to be a male trait under intersexual selection. Oxidative stress is the imbalance between the production of reactive oxygen species (ROS) during the course of aerobic metabolism in plants and animals and the production of antioxidant defenses (Costantini 2014). ROS damage important biomolecules (lipids, proteins, and DNA), and such damage has been linked to pathology and aging in humans (Finkel and Holbrook 2000). In animals, oxidative stress has been shown to increase during periods of intense reproductive investment in taxa as diverse as great tits, *Parus major* (Christe et al. 2012), white-browed sparrow weavers, *Plocepasser mahali* (Cram et al. 2014), eastern chipmunks, *Tamias striatus* (Bergeron et al. 2011), and northern elephant seals, *Mirounga angustirostris* (Sharick et al. 2014). Evidence from common yellowthroats, *Geothlypis trichas*, suggests that individuals with lower levels of oxidative damage have increased survivorship (Freeman-Gallant et al. 2011). Oxidative stress has thus been suggested to underlie life-history trade-offs involving future reproduction and longevity (Selman et al. 2012; Speakman and Garratt 2014). It has also been implicated as part of the mechanism via which honest advertising of individual quality is maintained in sexual selection—in regards to the development of ornaments and other sexual signals used to attract mates (Schantz et al. 1999; Alonso-Alvarez et al. 2007; Garratt and Brooks 2012; Noguera et al. 2012). In sum, both immunocompetence and oxidative balance can serve as important measures of male quality. The relationship of such measures to male dominance and male mating success, however, remains poorly studied among mammals outside the laboratory.

Primates are a particularly interesting and challenging taxon in which to examine how variation in male physiological quality may relate to dominance and mating success. They are long-lived and spend most of their lives in groups of relatively stable composition, where long-lasting intrasexual and intersexual social relationships may have important effects on reproductive strategies and fitness outcomes (Mitani et al. 2012). Although the behavioral, morphological, and endocrine aspects of male social status in primates are frequently examined, its immunological and oxidative correlates and their relationship to mating success are not. Data on wound healing suggest that in yellow baboons, *Papio cynocephalus*, higher-ranking males had more robust functional immune response (Archie et al. 2012). Higher-ranking mandrills, *Mandrillus sphinx*, had lower nonmating season levels of oxidative damage (Beaulieu et al. 2014). Mandrills, but not baboons, possess bright red sexual coloration on their faces. Mandrill females prefer mating with redder males, and even though redness also correlates with male dominance rank, female preference for redness was stronger than their preference for dominant males (Setchell 2005). Male coloration and measures of immune function or parasitism in mandrills, however, were not related (Setchell et al. 2009) leaving the functional significance of female preference for male redness in this species a puzzle.

Rhesus macaques, *Macaca mulatta*, form multimale–multifemale groups with female philopatry. Males disperse around puberty and sometimes change groups again later in life. Due to high estrous synchrony among females during their 5–6-month long breeding season (Vandenbergh and Vessey 1968; Dubuc et al. 2011), alpha male rhesus macaques cannot effectively monopolize mating activity. In the free-ranging rhesus macaque population on Cayo Santiago, although alpha males generally mate more and sire more infants than other males (Bercovitch and Nurnberg 1996; Paul 2004; Rodriguez-Llanes et al. 2009), reproductive skew is low to moderate (Curie Cohen et al. 1983; Berard et al. 1993; Dubuc et al. 2011).

Rhesus macaques have a moderate level of sexual dimorphism in body size (Smith and Jungers 1997), indicative of a diminished importance of male–male contest sexual competition (Plavcan 2012), and males have relatively large testes, suggesting that sperm competition is important in determining male reproductive success (Harcourt et al. 1981; Bercovitch and Rodriguez 1993). Male attempts at sexual coercion of females are inefficient (Manson 1992; Manson 1994) and females are sexually attracted to males with darker, redder facial coloration—a trait which is not associated with high rank (Higham et al. 2013; Dubuc et al. 2014a). Although there is evidence that high-ranking males are in better energetic condition than low-ranking ones (Higham et al. 2011), it is possible that some aspects of male quality are independent of rank and are advertised to females, for example, through red coloration.

Variation in male immune function and oxidative status have not been studied to date in free-ranging rhesus macaques, even though the presence of sexual skin coloration and its relationship to female mate preference and male fitness in this species suggest that these traits might be important. In this study, we thus aimed to: 1) quantify interindividual variation in immune function and oxidative status (used as indicators of quality) among the males of a group of free-ranging rhesus macaques; 2) examine the relationship between male quality and dominance; and 3) examine the relationship between male quality and mating success.

METHODS

Study site and subjects

The free-ranging rhesus macaques of Cayo Santiago Island in Puerto Rico are descendants of the monkeys originally introduced from India in 1938 (Rawlins and Kessler 1986). During the study period (November 2012–August 2013), the rhesus population on Cayo was approximately 1300 monkeys. There were 6 large and distinct and 3 less well-defined and smaller social groups in the population. All of our data were obtained from one of the distinctly defined larger groups, Group S. During the mating season Group S numbered 133 individuals including 15 adult males (≥ 5 years old) and 42 adult females (≥ 3 years old). Accurate ages and natal origin of our study subjects ($N = 15$ males) were known from long-term records of the Caribbean Primate Research Center (CPRC) of University of Puerto Rico. As of 1 March 2013 (the first full month of the mating season), they had a mean age of 8.4 years (standard error [SE] ± 0.7 ; range: 5.3–13.3; Supplementary Table S1). Six of the focal males were natal to their group and were yet to emigrate (mean age \pm SE = 5.9 ± 0.2 years; range: 5.3–6.4); 9 had immigrated into the group before ($N = 8$) or during ($N = 1$) this study (mean age \pm SE = 10.1 ± 2.5 years; range: 7.3–13.3).

Behavioral observations

We used focal sampling (of particular males) and behavioral sampling (of any male in the group in sight) to record all instances of agonism and copulations via continuous recording (Martin and Bateson 2007). Observations took place between 21 February and 16 August 2013. Only 4 copulations with 4 different females were observed in July and from birth records of subsequent offspring we estimated that the last potentially fertile copulation of the mating season occurred around 26 June. We thus define the mating season as the period between 21 February and 28 June. During the mating season, we collected focal data on 77 days totaling 326.6 h (Supplementary Table S1). We collected data 4–5 days a week, between 7:30–14:00 h. We conducted short (5 min in duration) but frequent (every 1–2 h) focal follows of all males to ensure that our behavioral data were representative of the focal subjects' activity levels throughout the day. Although this strategy reduced the total duration of focal data, we were able to collect (due to increased search effort at more frequent intervals, in comparison with e.g., 30-min or 1-h focal follows), it also ensured that focal observations were more temporally distributed for each focal subject.

Male mating success

Male rhesus macaques are multiple-mount ejaculators so not all copulations result in ejaculations. A full multiple-mount mating series can last up to 1 h (Manson 1996) so we were not always able to document the culmination of a mating series during our 5-min long focal follows. We thus used observations of all copulations (with and without ejaculation) to identify the maximum number of different females each focal subject mated with. Copulations recorded during focal follows and group-level observations were pooled. Although this metric does not provide reliable estimates of copulation rates and thus is not comparable with other studies using rate-based measures of mating success, we consider it more helpful for the purposes of estimating the maximum spread of a male's sexual network. A single copulation is sometimes sufficient to fertilize a female and so a male with a much higher copulation rate would not necessarily have higher reproductive success than a male who mated only once. Nevertheless, copulation rates calculated from focal data and total number of mating partners calculated from focal and group-level sampling were significantly correlated during this study ($r_s = 0.6$, $N = 15$ males, $P_{2\text{-tailed}} = 0.01$).

Although some behavioral measures of mating behavior (i.e., copulation rates and mate-guarding effort) are not a reliable indicator of the actual sire in specific conception events in rhesus macaques (Dubuc et al. 2011, 2012), the total number of females mated with, when adjusted for conception probability, correlates well with actual relative reproductive success in male rhesus macaques (Bercovitch and Nurnberg 1996). For each focal male, we thus calculated the total number of fertile females in Group S mated with as our measure of male mating success. For each female, we defined a "potentially fertile window" as the time between 180 and 160 days before parturition. Average gestation length in rhesus macaques is $166.5 \pm$ standard deviation 7.4 days ($N = 709$; range: 133–200 days). As 80% of pregnancies last 160–175 days (Silk et al. 1993), we chose the 160th day before birth as the upper cut-off point for potentially fertile copulations. To account for the possibility that sperm may survive in the females' reproductive tract for several days before fertilization occurs, we allowed 5 days before the lower end of the 175–160 day range and thus considered only copulations after the 180th day before parturition as potentially fertile.

Females were visually identifiable as being pregnant during the study (by a temporary change in facial color; as well as extended abdomens) and births were monitored 5 days a week by multiple observers. We estimate that the likelihood of omitting any births due to stillbirth or infant death within a few days of birth, without it being noted was therefore minimal. From a total of 41 females over the age of 3 in Group S (as of 1 March 2014; mean age = $7.9 \pm$ SE 0.75 years; range: 3.1–23.0), 29 produced young (mean age = $7.7 \pm$ SE 0.7 years; range: 3.3–18.1). Interindividual differences in male focal observation time (observation bias) were not related to our measure of mating success, the total number of potentially fertile females mated with ($r_s = 0.39$, $N = 15$, $P_{2\text{-tailed}} = 0.15$).

Male dominance relations

Dyadic agonistic interactions among focal males ($N = 525$) were recorded at all times during the mating season (March–June 2013). Dominance interactions included unprovoked submissions, displacements, threats, charges, chases, and contact aggression. Relative male dominance was assessed by calculating the number of males in the group that each individual was able to dominate in dyadic agonistic interactions more often than they were able to dominate him (Hemelrijk et al. 2005) with the package DomiCalc (Schmid and de Vries 2013).

Measures of male quality

Animal trapping procedure

To quantify immune function and oxidative status, we collected blood samples from our study subjects. The 15 focal males were trapped over a period of 59 days (28 November 2012–4 February 2013) prior to the start of mating season by trained CPRC staff inside feeding corrals. Animals were trapped in the morning, between 8 AM and 12 PM, sedated with ketamine (~10 mg/kg via intramuscular injection), and placed in a standard squeeze cage. Blood samples were collected from the femoral vein by veterinary technicians. After recording morphometric data (crown-rump length, abdominal skinfold thickness, subscapular skinfold thickness, body weight), subjects were monitored in their cages until recovery from anesthesia. In the afternoon, males were released near their group. Four individuals spent a night in the cages and were processed the following morning. At the time of trapping, males were also inspected for wounds, which were described in written notes and photographed. All animal handling procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico, Medical Sciences Campus.

Innate immune function measures

Assays for innate immune function are widely used in ecoimmunology to characterize individual variation in the ability to respond to infection (Liebl and Martin 2009; Demas et al. 2011; Brock et al. 2014; Prall and Muehlenbein 2014). Even though such assays only assess 1 particular facet of the complex immune system of vertebrates (i.e., innate or constitutive immunity) and thus they cannot produce a comprehensive index of an individual's overall immunocompetence, meaningful relationships between innate immune function assay results and traits indicative of individual's quality and/or health have been documented in several species. For example, among American crows, *Corvus brachyrhynchos*, more inbred individuals were in poorer condition, had lower measures of innate immune function (measured via a bacteria killing assay), and higher disease-related mortality (Townsend et al. 2010). In Florida scrub jays, *Aphelocoma coerulescens*, male breeders who showed higher

innate immune activity were more likely to survive an epidemic of eastern encephalitis that killed 39% of the study population (Wilcoxon et al. 2010). Such assay techniques have been applied to mammals less often but a study of female African buffalo, *Syncerus caffer*, showed that animals with higher innate immune activity had fewer ticks (Anderson et al. 2013).

Bacterial killing assay. We assessed innate immunity in serum via ex vivo bacterial killing assays (BKA; Table 1). This assay measures the functional ability of integrative immunological components, including opsonizing proteins and antibodies, to lyse a known quantity of *Escherichia coli* bacteria (ATCC # 8739) relative to a positive control (Millet et al. 2007; Demas et al. 2011). After a test run to optimize dilutions, we diluted serum 1:250 in L-glutamine supplemented CO₂ Independent media (Gibco #18045). We reconstituted a single lyophilized *E. coli* pellet (MicroBiologics Epower Microorganisms #0483E7) in sterile saline and then diluted it to a working solution, which produced approximately 200–300 colonies per 20 µL of aliquot. We added aliquots of bacterial working solution to diluted serum in a microcentrifuge tube, vortexed the tube, and incubated it for 30 min. After incubation, we spread samples on trypticase soy agar

plates (BD BBL #211043) in triplicate and incubated overnight. We counted the number of colonies for each plate the next day and calculated percent bacterial killing for each sample relative to a positive control (media and bacteria only).

Hemolytic complement assay. We also used serum to measure the classical pathway of complement protein activity (Table 1) via a hemolytic complement assay (HCA) (Sinclair and Lochmiller 2000; Demas et al. 2011). In this assay, after test runs to optimize dilutions, we diluted serum 1:200 and 1:400 in dextrose gelatin veronal buffer (Lonza BioWhittaker #10–539) and pipetted it in duplicate onto a round-bottom 96-well plate. We diluted a 100% sheep red blood cell solution (Rockland #R406-0100) to 20% and washed it in sterile saline, and diluted it again a 1% solution in veronal buffer. We diluted anti-sheep red blood cell antibodies (Sigma #S1389-1VL) 1:40 in veronal buffer. We then added both diluted antibodies and sheep red blood cells to each sample well, and vortexed the plate. Following incubation for 1.5 h, we centrifuged the plate and transferred the supernatant to a new 96 well round bottom plate. We read absorbance of this supernatant at 405 nm. Results of this assay are expressed as CH50 units, or the inverse of the dilution predicted to cause 50% hemolysis (Mayer 1948).

Table 1

Measures of immune function, oxidative status, and confounding variables used to assess male quality in this study

Measure	Rationale and significance	Results (this study)	References
Main measures used to characterize male immune function and oxidative status			
BKA	An in vitro assay of innate immune function. Measures the ability of natural antibodies, opsonizing proteins, and various antimicrobials to lyse a known quantity of bacteria.	Positively correlated with dominance and mating success.	Pral and Muehlenbein (2014), Demas et al. (2011), Liebl and Martin (2009), Millet et al. (2007)
HCA	An in vitro assay of innate immune function. Measures the ability of the antibody-dependent pathway of the complement system to lyse sheep red blood cells. The complement system is part of the innate immune system that consists of plasma proteins involved in the formation of a protein complex (membrane attack complex) that lyses pathogens.	Positively correlated with dominance.	Pral and Muehlenbein (2014), Demas et al. (2011)
Oxidative stress assay	The TBARS assay measures lipid peroxidation in plasma as an index of oxidative damage.	Negatively correlated with dominance and mating success.	Bergeron et al. (2011), Torres and Velando (2007), Speakman and Garratt (2014)
Measures of possible confounding effects on the relationships between male dominance status and the main variables of interest			
Testosterone assay	Steroid hormone: responsible for the sexual development and reproductive function in males. Hypothesized to have immune-suppressive properties and thus might have a confounding effect on any relationship between immune function and dominance status.	No relationship: male dominance status, BKA, HCA, oxidative damage.	Pral and Muehlenbein (2014), Muehlenbein and Bribiescas (2005)
Cortisol assay	Glucocorticoid hormone, which is a key component of the physiological stress response and is known to also regulate immune function at several levels. Has anti-inflammatory properties. Can probably affect measures of BKA and possibly HCA.	No relationship: male dominance status, BKA, HCA, oxidative damage.	Martin (2009), Brooks and Mateo (2013), Ebensperger et al. (2015);
Fresh or healing injuries	Presence of fresh injuries is associated with immune activation that facilitates wound healing.	Males with fresh or healing injuries did not differ from those without such injuries in their BKA and HCA scores.	Neuman-Lee and French (2014), Roupe et al. (2010)
CRP assay	Central component of the acute phase response of the immune system; nonspecific response to infection or injury—the first physiological line of defense against pathogens. High levels of CRP are indicative of inflammation and are predictive of cardiovascular disease risk in humans. We measured CRP levels to assess current male inflammation status as a possible confound of our 2 principal innate immune function measures (BKA and HCA).	No relationship with male dominance status or BKA. Correlated with HCA scores; males with fresh or healing injuries had slightly higher CRP but not significantly so.	Pepys and Hirschfield (2003), Ridker et al. (2000), Gruenewald et al. (2006), Black et al. (2004)

Oxidative stress measure

We used the OXitek TBARS Assay Kit (ZeptoMetrics Corporation, #0801192) to quantify lipid peroxidation in plasma samples as a measure of oxidative damage (measured in Malondialdehyde (MDA) equivalents, nmol/mL), following the manufacturer's instructions. This assay is one of the more commonly used in animal studies to assess costs of reproduction both in the laboratory and in the field (Speakman and Garratt 2014; Tables 1 and 2). Samples were assayed in duplicate. Two values were excluded from analysis because their coefficients of variation (CVs) from duplicate samples were more than 15% and we did not have sufficient plasma to rerun the samples. One sample was excluded from analysis because its value was more than 29 standard deviations higher than the mean value of the remaining values (sample value = 30.59; mean of all the 12 remaining samples = 2.54 ± 0.28). Mean CV for the samples included in further analyses was thus $4.55\% \pm SE 1.28$ (range: 0–10.46; $N = 12$ males).

Confounding effects of endocrinological profiles and inflammation

To account for potential confounding effects, we examined if our measures of immunity or oxidative status were affected by hormone profiles (plasma cortisol and testosterone). Additionally, as both innate immune function and oxidative damage may increase in response to inflammation, we also examined whether the presence of fresh/healing wounds and levels of C-reactive protein (CRP), a marker of inflammation (Pepys and Hirschfield 2003), affected our measures of male quality (Table 1).

Hormone and CRP assays

We assayed testosterone and cortisol in serum and CRP in plasma, collected at the same time as the samples used for the other assays. Steroids were assessed with enzyme-immunoassay reagents and protocols obtained from the Clinical Endocrinology Laboratory at the University of California at Davis (T antibody R156/7, cortisol antibody R4866). For the CRP assay, we used commercially available Monkey CRP ELISA kits (Life Diagnostics, Inc. #2210-4). All assays were run in duplicate (1 plate per assay). Intra-assay CVs measured from duplicates were: $3.57\% \pm SE 0.63$ (range: 0–5.45%) for the calculated testosterone values and $5.33\% \pm SE 2.60$ (range: 0–6.9%) for the calculated cortisol values. For the CRP assay, 5 of the focal subjects' samples had CVs greater than 15% or produced unreliable readings otherwise so were excluded from analysis. The CVs among the resulting data set ($N = 10$) averaged: $5.14\% \pm SE 1.11$ (range: 0.11–10.15%).

BKA scores did not correlate with cortisol (Kendall rank-order correlation test: $\tau = -0.143$, $N = 15$; $P = 0.49$) or with testosterone levels ($\tau = 0.03$, $N = 15$, $P = 0.92$). HCA scores did not correlate with cortisol ($\tau = 0.10$, $N = 14$, $P = 0.66$) or testosterone ($\tau = 0.28$, $N = 14$, $P = 0.19$). Oxidative stress levels did not correlate with male endocrine profiles either (cortisol: $\tau = -0.02$, $N = 12$; $P = 1.00$; testosterone: $\tau = -0.23$, $N = 12$, $P = 0.34$). Seven of the males had fresh or healing wounds on the day of sample collection (small scratches were not included), and one of them had to receive minor veterinary treatment. Although mean BKA scores were higher among the wounded ($56.84\% \pm SE 15.03$) than the nonwounded ($36.67\% \pm SE 10.29$), the difference was not statistically significant (Mann–Whitney U [MWU] test: $z = 1.39$; $N = 15$; $P = 0.17$). Wounded and nonwounded males also did not differ in their HCA scores (MWU test: $z = 0.96$; $N = 14$; $P = 0.34$) or in oxidative stress levels ($z = -0.60$; $N = 12$; $P = 0.55$). On average, males with

fresh/healing wounds had somewhat higher CRP levels than males without wounds, but the difference was not statistically significant (MWU test: $z = 1.36$; $N = 10$; $P = 0.18$). BKA scores ($\tau = -0.07$, $N = 10$, $P = 0.86$) and oxidative stress levels ($\tau = -0.07$, $N = 8$, $P = 0.90$) did not correlate significantly with CRP levels but HCA scores did ($\tau = 0.6$, $N = 10$, $P = 0.02$). However, CRP levels did not correlate with male dominance status ($\tau = 0.48$, $N = 10$, $P = 0.07$), so any relationship between HCA and rank was unlikely to be confounded by inflammation status. In sum, our explorative analysis of any biases in measurement of male quality via innate immune function and oxidative status did not reveal any major confounds.

Data analysis

Because of small sample size (range: 12–15 unique male blood samples), we used nonparametric tests. We carried out pair-wise Kendall rank-order correlations and partial Kendall rank-order correlations in R version 3.0.3 (R Core Team 2014) with the Kendall (McLeod 2011) and ppcor (Kim 2012) packages, respectively. All tests were 2-tailed.

RESULTS

Were male immune function and oxidative status related to dominance?

Relative male dominance correlated significantly with all 3 measures of physiological condition. Higher-ranking males had higher BKA (Kendall rank-order correlation test: $\tau = 0.44$, $N = 15$, $P = 0.03$; Figure 1a) and HCA scores ($\tau = 0.53$, $N = 14$, $P = 0.01$; Figure 1b) and lower levels of lipid peroxidation ($\tau = -0.55$, $N = 12$, $P = 0.02$; Figure 1c). The alpha male, in particular, who immigrated into the group at the start of the mating season and took over the top position via direct aggressive challenge, had the second highest BKA score (99.01%) after the former alpha; the highest HCA scores (211.6 CH50 units), and the lowest levels of oxidative damage (1.64 MDA nm/mL). Male age, however, also correlated with 1 of the 2 measures of immune function and with oxidative status: older males had higher BKA scores ($\tau = 0.48$, $N = 15$, $P = 0.02$) and lower levels of lipid peroxidation ($\tau = -0.47$, $N = 12$, $P = 0.04$). HCA scores were not correlated with age ($\tau = 0.11$; $N = 14$; $P = 0.62$). After controlling for the potential confounding effect of age, male dominance was still significantly correlated with BKA scores (partial Kendall correlation test: $\tau = 0.44$, $N = 15$, $P = 0.03$) and with lipid peroxidation (partial $\tau = -0.57$; $N = 12$; $P = 0.02$).

Was mating success related to male immune function and oxidative status?

Male mating success correlated positively and significantly with male BKA scores ($\tau = 0.53$, $N = 15$, $P = 0.01$) and positively but not significantly with HCA scores ($\tau = 0.41$, $N = 14$, $P = 0.06$). Male mating success also correlated negatively and significantly with lipid peroxidation levels ($\tau = -0.58$, $N = 12$, $P = 0.02$). Thus, males with more functional innate immune system, measured via bacterial killing activity, and lower oxidative damage had high mating success. Two potential factors that might affect male mating success in rhesus macaques are age and dominance status. In our sample, only male dominance status correlated with the total number of fertile mating partners ($\tau = 0.56$, $N = 15$, $P = 0.009$). Age was not significantly correlated with mating success ($\tau = 0.40$, $N = 15$, $P = 0.06$) and we did not consider its effect further. We

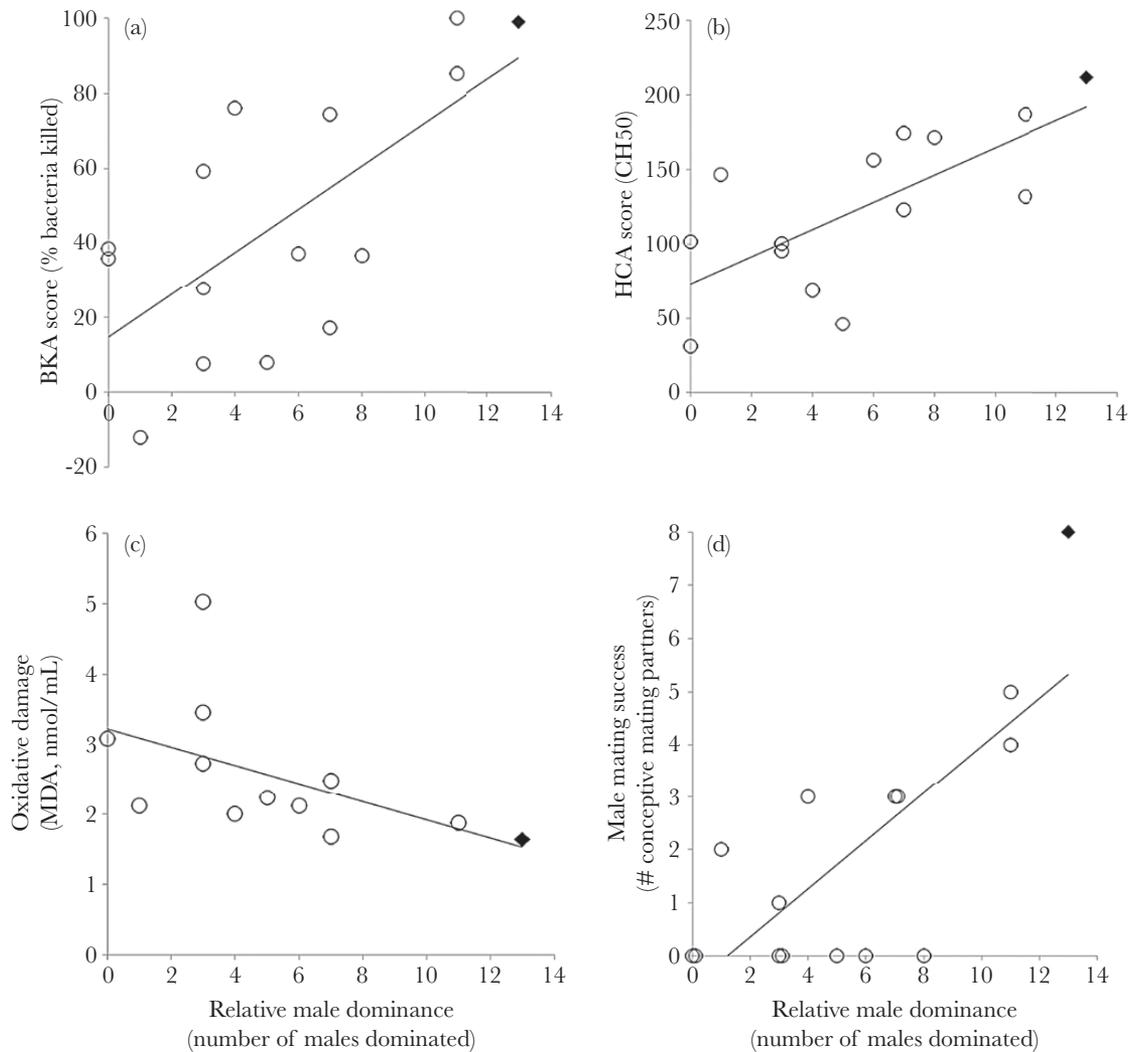


Figure 1

Relationship between male dominance (from left to right: low to high rank) and (a) bacterial killing activity (BKA) assay scores, (b) hemolytic complement activity (HCA) assay scores, (c) oxidative damage levels, and (d) mating success. The alpha male (11Z) is marked by a filled diamond. Some of the data points in Figure 1d are jittered to avoid overplotting.

reexamined the relationship between male condition and mating success, while controlling for male dominance in partial correlations. BKA scores (partial $\tau = 0.38$, $N = 15$, $P = 0.06$) and oxidative status (partial $\tau = -0.38$, $N = 12$, $P = 0.1$) were no longer significantly correlated with mating success, after the effect of male dominance was taken into account.

DISCUSSION

Our data on interindividual differences in immunocompetence and oxidative stress levels showed that more dominant rhesus macaque males were in better condition at the onset of the mating season: they had more robust innate immune function response and lower levels of lipid peroxidation. Higher-ranking males also mated with a greater number of potentially fertile females during the mating season so that our physiological measures of individual quality were also correlated with mating success. However, after controlling for male rank, male physiological quality was no longer associated with mating success. We first discuss several plausible explanations for the observed relationship between male rank and quality. We then

examine the implications of our results for the possible interplay between mechanisms of male–male competition and female choice in this species and suggest several important directions for future research into sexual selection, acting on male quality.

Male dominance in intrasexual competition has previously been linked to greater immunocompetence in a number of species, including in field crickets, *Gryllus bimaculatus*, (Rantala and Kortet 2004), burying beetles, *Nicrophorus orbicollis*, (Steiger et al. 2012), drumming wolf spiders, *Hygrolycosa rubrofasciata*, (Ahtiainen et al. 2006), red jungle fowl, *Gallus gallus*, (Zuk and Johnsen 2000), and house finches, *Carpodacus mexicanus* (Hawley et al. 2006, 2007). A review of studies examining the relationship between social status and immune function in animals showed substantial variation in the type of measure used to assess immunity, as well as in the presence and the direction of a relationship between immunity and social status (Cavigelli and Chaudhry 2012). Few studies of free-ranging social mammals exist (except those relying on fecal measures of parasitism as a proxy for immune function) and both of them were conducted in baboons (Cavigelli and Chaudhry 2012). These studies showed that higher-ranking males had greater

immunocompetence as indicated by 1) lower incidence of illness and faster wound healing (yellow baboons, *Papio cynocephalus*—Archie et al. 2012) and 2) higher lymphocyte counts (olive baboons, *Papio anubis*—Sapolsky 1993), in comparison with lower-ranking individuals. An experiment with captive long-tailed macaques, *Macaca fascicularis*, similarly suggests that immunocompetence might be compromised among low-ranking males, who were significantly more likely to contract a respiratory infection than higher-ranking males, even though a functional measure of immune function (lymphocyte proliferation) was not related to social status (Cohen et al. 1997). Our results are in line with these findings and extend the study of ecoimmunology of primates both taxonomically and in terms of the laboratory techniques used to assess immune function (bacteria killing and HCAs).

Studies of the relationship between dominance status and oxidative stress in vertebrates are rarer still and have thus far considered primarily solitary or pair-breeding species. White skink males, *Egernia whitii*, exhibiting high rates of aggressive behavior, for example, showed increased antioxidant defenses and did not suffer from an increase in oxidative damage (Isaksson et al. 2011). This study did not address the dominance status of individual white skinks, specifically, but high rates of aggressive behavior are typical of more dominant individuals in many vertebrates. In a cooperative breeder, the white-browed weaver, *Plocepasser mahali*, dominant males did not differ in either antioxidant protection or oxidative damage from subordinates and the observed decline in antioxidant protection after the breeding season was unrelated to dominance status (Cram et al. 2014). Nevertheless, some studies find that more dominant individuals have superior oxidative status: for example, honey bee queens (Haddad et al. 2007). The causal direction in such relationships is not always clear, however. Although it is plausible that superior oxidative status may allow individuals to invest more heavily in status competition and thus become higher ranking, it is equally plausible that the attainment of high-social status may result in oxidative benefits. Evidence for the latter comes from an experimental manipulation of plumage color in female North American barn swallows. After making some females darker (a trait associated with dominance), these females experienced a reduction in oxidative damage, likely because they received fewer challenges from competitors during the breeding season (Vitousek et al. 2013). The only field primate study to date to employ a measure of oxidative stress found that among free-ranging mandrills, *Mandrillus sphinx*, higher-ranking males had lower oxidative damage before the start of the mating season and were the only males to suffer an increase in oxidative damage during the mating season (Beaulieu et al. 2014). Our data on lipid peroxidation among male rhesus macaques measured before the start of the mating season are in agreement with the mandrill findings, in that higher-ranking males had lower levels of oxidative damage outside the breeding season.

The broad agreement between the findings of our study and the results on wound healing among baboons (Archie et al. 2012), and oxidative stress in mandrills (Beaulieu et al. 2014), suggests that despite some differences in the mating system and the dynamics of intermale dominance relations among these 3 species, measures of male quality (immune function and oxidative balance) may be related in a similar manner to social status.

We suggest 3 nonmutually exclusive explanations for the observed relationship between male rank and physiological measures of quality in rhesus macaques: 1) interindividual differences in energetic condition; 2) nonenergetic, psychosocial benefits of

high-social status; and 3) underlying genetic quality of higher-ranking animals.

First, interindividual differences in male energetic condition may mediate differences in immune functionality, as the availability of energetic resources can affect an animal's ability to maintain a functional immune system and mount an effective immune response (Lochmiller and Deerenberg 2000; Demas 2004; Demas et al. 2012). Food availability has been shown to affect oxidative stress balance in wild insectivorous birds (van de Crommenacker et al. 2011) so better energetic condition could also improve the ability to resist and repair oxidative damage. The Cayo Santiago rhesus macaques are provisioned with monkey chow on a daily basis, but still not all individuals have equal access to the food. Higher-ranking males from an earlier study of a larger group on the island spent more time feeding on high-energy monkey chow during the birth season than lower-ranking individuals and as a result had higher body mass index (BMI) at the onset of the mating season (Higham et al. 2011). In our data set, however, male dominance rank was unrelated to either BMI or abdominal skinfold thickness, 2 key measures of condition (Georgiev et al., unpublished data). Energetic condition, therefore, would not fully explain why higher-ranking males had more functional innate immune system and lower oxidative damage in our data set.

Second, nonenergetic, psychosocial factors may also account for the relationship between male dominance status and individual quality. Changes in the expression of genes involved in the immune response have been experimentally induced in captive female rhesus macaques by manipulating their dominance status (Tung et al. 2012) suggesting that the social environment alone, independently from energetic condition, may affect an individual's ability to cope with infection. Importantly, Tung et al. (2012) showed that it was the attainment of high rank that led to beneficial modifications in immune function, rather than that highly functional immune system was a prerequisite for becoming a highly ranked female. Higher-ranking males on Cayo tend to be less restless and to engage in self-scratching less frequently than lower-ranking males (Higham et al. 2011), indicating that they may not be as psycho-socially stressed (Maestripieri et al. 1992) as lower-ranking individuals. High-ranking males are thus not expected to have higher circulating levels of cortisol in this species, particularly during the socially stable nonmating season, when our measures of male quality were obtained. Cortisol levels in our data set were not related to immune function scores or to lipid peroxidation, suggesting that psychosocial stress was not the primary determinant of interindividual differences in male quality at the end of the nonmating season.

Third, the association between male quality and high dominance rank may be due to the underlying genetic traits of the higher-ranking males in our sample. This explanation is not mutually exclusive to the previous 2, but a genetic mechanism for the inheritance of the “quality” of the sire is essential if female mate choice for indirect benefits is to occur (Moller and Alatalo 1999; Neff and Pitcher 2004). Behavioral female choice in rhesus macaques is known to be effective (Manson 1992). The fact that females paid preferential attention to male faces that are more symmetrical and redder (Waitt et al. 2003; Waitt and Little 2006) under experimental conditions, and that females on Cayo Santiago directed more sexual solicitations at males with darker, redder faces (Dubuc et al. 2014a) suggests that females may be exercising choice for good genes. Facial coloration and symmetry are hypothesized to be linked to current physiological health and to developmental stability, respectively (Changizi et al. 2006; Bradley and Mundy 2008; Little et al.

2011), so these traits might function as honest signals of male quality in rhesus macaques. Darker, redder males on Cayo Santiago, who are also higher ranking, have increased reproductive success and facial color shows moderate heritability (Dubuc et al. 2014b). Whether male facial traits are associated with immunocompetence and oxidative status, however, remains to be established. Testing the relationships among female mating preferences, male facial traits (color and symmetry), and physiological markers of male quality is therefore an important direction for future research.

In our study, we also found that males with higher BKA scores and lower levels of lipid peroxidation mated with more potentially fertile females during the subsequent mating season. Our measure of mating success was also correlated with male dominance and when the effect of rank was accounted for the correlations between indices of male quality and mating success were no longer significant. To conclude that active female mate choice for males with high immunocompetence and low oxidative damage does not occur in rhesus macaques, however, would be premature. Even though female rhesus can be targeted aggressively by higher-ranking males when they maintain proximity to lower-ranking males, they do not then copulate with the aggressors and instead successfully exercise their choice by restoring proximity to their original lower-ranking consorts (Manson 1992, 1994). Females can also refuse to mate by not cooperating with a male who solicits copulation (Manson 1992). Thus, even though male rank was more strongly correlated with measures of quality than mating success was, ruling out the role of female choice for high-quality mates based on this evidence would not be consistent with previous research on the ability of females to resist mating with dominant males or with our own observations. To clarify the role of female mate choice for high-quality males, a detailed study of female mating preferences is needed, ideally focusing on females as focal subjects and tracking the timing of ovulation via noninvasive hormonal sampling.

In conclusion, our study showed that higher-ranking males in a group-living mammal have more robust innate immune response and lower levels of oxidative damage. Associations between measures of male quality and mating success suggest that female mate choice for good genes may operate in this species, but this hypothesis remains to be tested with detailed behavioral, physiological, and genetic data. The associations between quality, rank, and mating success reported in this study should be further investigated in studies in which condition or rank is experimentally manipulated. Such studies could enhance our understanding of mating strategies of rhesus macaques, and this species' mating system. Further research on male quality, male–male competition, and mating success in nonhuman primates can also contribute to our understanding of the dynamics and processes of sexual selection in socially living vertebrates.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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