

The Costs of Reproductive Success in Male Rhesus Macaques (*Macaca mulatta*) on Cayo Santiago

James P. Higham · Dario Maestriperieri

Received: 24 May 2013 / Accepted: 28 June 2014 / Published online: 29 July 2014
© Springer Science+Business Media New York 2014

Abstract Sexual selection acts to increase the success of males possessing advantageous traits in competition over females. In primates, interspecific variability in social and mating systems creates highly variable selective pressures on males, changing the relative strength of both intra- and intersexual selection, and the relative degree of direct vs. indirect male–male competition. Rhesus macaques are an interesting species for studying intrasexual selection and male–male competition, because they exhibit relatively low (for Papionini) body and canine size dimorphism, and exhibit large testes, suggesting reduced direct competition and strong indirect competition. We have undertaken several studies of male rhesus macaques on Cayo Santiago, from analyses of long-term life-history data to shorter term projects that combined noninvasive measures of physiological markers such as concentrations of urinary C-peptide of insulin and androgen and glucocorticoid (GC) concentrations, with measures of behavior and of sexually selected signals (male red facial coloration). We here review these studies, combining data from short-term studies with long-term mortality data to present an integrated picture of both the short- and long-term gross costs of male mating competition. We find that males exhibit many signs of the costs of indirect competition, such as energetic consequences of reduced feeding and high copulation rates. During periods of more direct contest, such as during dominance instability, males are also characterized by high androgen and GC concentrations among high-ranking individuals. Consistent with relatively weak direct male–male competition, male red skin coloration appears to be more related to female choice (intersexual selection) than the signaling of dominance status (intrasexual selection). Forty-five years of life-history data show that male mortality is higher during the mating than the birth season, a pattern we hypothesize to be linked to the costs associated with mating activity. We finish by discussing unresolved issues, such as the costs of sperm competition and the data that are needed to address them.

J. P. Higham (✉)

Department of Anthropology, New York University, New York, New York 10003, USA
e-mail: jhigham@nyu.edu

D. Maestriperieri

Institute for Mind and Biology, The University of Chicago, Chicago, Illinois 60637, USA

Keywords Reproductive success · Male-male competition · Urinary C-peptide · Rhesus macaques · Endurance rivalry

Introduction

Darwin (1871) identified two sexual selection processes: intrasexual selection, in which individuals of one sex compete with each other over access to members of the other sex; and intersexual selection, in which individuals of one sex choose members of the other sex as mating partners. These two processes tend to produce different types of male adaptations for mating competition. Intrasexual selection among males tends to produce weaponry such as the antlers of male deer and the huge canines of male mandrills, whereas intersexual selection related to mate choice between males and females leads to the evolution of ornaments such as the peacock's tail and the bright colors of male birds of paradise (Clutton-Brock and McAuliffe 2009). However, male-male competition may under certain circumstances take indirect rather than direct forms. Instead of leading to the evolution of weaponry, indirect competition leads to the evolution of traits related to processes such as sperm competition, e.g., large testis size (Harcourt *et al.* 1981) and endurance rivalry (Andersson 1994), in which reproductive success is determined by the ability of males to endure in competition over time, e.g., traits related to efficiency in feeding and fat accumulation, and stamina. In addition, reduced direct competition among males and an absence of sexual dimorphism in strength and weaponry increases the potential scope for direct female choice and processes of intersexual selection.

Variation in the social and mating systems of a species or population plays an important role in determining the type of sexual selection processes males experience, and hence male adaptations for mating competition. In nonhuman primates, the high degree of interspecific variability in social and mating systems is associated with significant variability in the type and intensity of male intrasexual competition, and in turn, with male traits (van Noordwijk and van Schaik 2004). Monogamous species exhibit low levels of body and canine size sexual dimorphism, as well as small testis size (Harcourt *et al.* 1981, 1995; Plavcan 1997, 2001, 2004; Plavcan and van Schaik 1992). In systems of unimale multifemale groups, males exhibit large body size and large canines, necessary for direct competition and to aggressively acquire and maintain multiple females, but small testes, consistent with low levels of sperm competition and indirect competition, as a result of an absence of intragroup competitors (Harcourt *et al.* 1981, 1995; Plavcan 1997, 2001, 2004; Plavcan and van Schaik 1992). In multimale multifemale groups, body and canine size dimorphism are typically intermediate (though dimorphism is highly variable, and on average closer to that seen in unimale rather than in monogamous systems), while testis size is large, as a result of intense sperm competition (Harcourt *et al.* 1981, 1995; Plavcan 1997, 2001, 2004; Plavcan and van Schaik 1992). This morphological variation reflects the degree of direct vs. indirect competition experienced by males living in different social and mating systems.

Although these general patterns have been demonstrated, they mask more subtle variation. Even among species exhibiting multimale multifemale groups, there is still a high degree of variation in body and canine size dimorphism and in testis size (Plavcan 2011). Much of this variation has been attributed to the relative synchrony of female

fertile periods (Dubuc *et al.* 2013; van Noordwijk and van Schaik 2004). When female menstrual cycles are asynchronous within a group, high-ranking males can monopolize fertile females and this tends to lead to strong reproductive skew (Gogarten and Koenig 2013; Kutsukake and Nunn 2006; Ostner *et al.* 2008) and strong direct contest competition over dominance rank with “top entry,” in which males enter the group and gain high status by challenging the alpha male directly (van Noordwijk and van Schaik 2004; Dubuc *et al.* 2013). When female cycles are highly synchronous, reproductive skew by male dominance tends to be lower, until the pay-offs for being high-ranking are reduced to the extent that males no longer fight directly over it. Instead they adopt queuing systems whereby new males are initially peripheral to the group and gradually rise in rank over time as higher-ranked individuals die or emigrate (Dubuc *et al.* 2013; van Noordwijk and van Schaik 2004;).

The rhesus macaques (*Macaca mulatta*) on Cayo Santiago show a strong degree of synchrony in female reproduction as a result of both large group sizes and reproductive seasonality (Berard *et al.* 1994; Hoffman *et al.* 2008, 2010; Rawlins and Kessler 1986). Reproductive skew by male dominance is consequently known to be low and variable, with alpha males obtaining around 20–30% of sired offspring (Berard *et al.* 1994; Dubuc *et al.* 2011, 2014a; Widdig *et al.* 2001), compared to much higher values for more sexually dimorphic Papionins such as mandrills (*Mandrillus sphinx*, 69%: Setchell *et al.* 2005; 76%: Charpentier *et al.* 2005). Consistent with low reproductive skew, in which fights over dominance are unlikely to have significant reproductive payoffs, males on Cayo Santiago do not exhibit “top-entry,” but adopt a queuing system (Manson 1995). Though it is possible that this is an artificial effect of unusually large group sizes, food provisioning, or an absence of predation, rhesus macaque morphology is also consistent with the hypothesis that they have reduced direct contest competition. Compared to other Papionini, rhesus macaques exhibit relatively low body and canine size sexual dimorphism, suggesting reduced direct competition (Plavcan 2004). Further, rhesus males exhibit relatively large testis size (Harcourt *et al.* 1981), consistent with increased indirect competition.

Given these particular dynamics, we might expect a particular type of cost to be associated with male rhesus macaque strategies. The presence of high levels of female synchrony means that the ability of high-ranking males to monopolize female reproduction is reduced and the percentage share of sired offspring obtained by such males is low, reducing the selective pressures on males to compete for dominance. In the absence of strong direct competition over dominance, it has been suggested that males should compete largely through a system of endurance rivalry (Bercovitch 1992, 1997), while given the large testis volume in this species, sperm competition has also been suggested as an important mechanism of indirect competition (Muehlenbein *et al.* 2002). Consistent with this, rhesus macaque males do not usually fight directly over access to females, but instead engage in periods of consortship and the following of females to obtain matings (Berard *et al.* 1994). As the mating season lasts for several months, the ability of males to undertake such behaviors may be restricted by male energetics, and the overall success of males determined by differences in their ability to endure in these types of competition over time. Under such a system we might also predict variation in male tactics, with sneak matings employed by those males not able

to undertake more costly strategies. Consistent with this, behavioral research on Cayo Santiago has shown that males sometimes undertake consortships (often necessary for serial mount copulations), but in the absence of consortships, males carry out sneak copulations (Berard *et al.* 1994). Given the reduced sexual dimorphism in body size, females are relatively free to exert a strong degree of mate choice. They are highly polyandrous and often mate with low-ranking males (Berard *et al.* 1994; Bercovitch 1992, 1997; Manson 1995). These mating patterns are what one would expect in a species in which males do not fight over dominance; when dominance is mainly a function of residency length, it seems unlikely to reflect male quality in the same way that dominance might among those species where males have fought directly to become dominant (Dubuc *et al.* 2013; Higham *et al.* 2012).

The aim of the present review is to synthesize the previous findings of our studies of male–male reproductive competition on Cayo Santiago. We combine data on male behavior and physiology collected during a short-term study with longer term mortality data collected by the Caribbean Primate Research Center over a 45-year period. Given the relatively high importance of indirect competition in rhesus macaques compared to many mammals, we recorded male energetic status in addition to measures of steroid hormones (glucocorticoids [GCs]; androgens) and behavior. After a presentation of our methods, we discuss the birth season, as this is the period in which males are not competing over females, and in which they may be able to build their condition. We then go on to look at the costs of indirect and direct competition that males experience during the mating season, then look at sexually selected traits, before linking the behavioral and physiological data to life history by looking at long-term mortality data. We conclude with general discussion on male rhesus macaque strategies before discussing future avenues of research.

Study Site and Methods

The studies described all occurred on Cayo Santiago, Puerto Rico. A rhesus macaque colony was established on Cayo Santiago in 1938 using free-ranging individuals from India (Rawlins and Kessler 1986). Macaques range freely in naturally formed social groups, but are provisioned with commercial monkey chow. Reproduction is seasonal, and though the timing of the reproductive seasons has been shifting over the years, during the study period there was a 6-mo mating season from March to August, and a 6-mo birth season from September to February. We collected behavioral and physiological data from October 2008 to August 2009. We had 15 focal males for the birth season and 20 focal males for the mating season, with 12 males present in both samples. A central aspect of this study was the assessment of male energetic status and body condition through the collection of urine samples for the measurement of the C-peptide of insulin (hereafter UCP). We validated the use of this marker in macaques by showing relationships between UCP concentrations and levels of body fat and body mass index (BMI), as well as by showing responsiveness to changes in diet (Girard-Buttoz *et al.* 2011). We also tested different sample treatment and storage methods (Higham *et al.* 2011a). In addition to urine samples for UCP measurement, we also collected fecal samples for the assessment of glucocorticoid (GC) and androgen concentrations using validated assays (Higham *et al.* 2013a). We also collected

behavioral data using continuous focal sampling and data on avoidances, displacements, fear grins, and agonistic interactions for the calculation of dominance rank (Higham and Maestripieri 2010; Higham *et al.* 2011b). During January and February of 2009, we trapped focal individuals and obtained morphometric measures, from which we calculated BMI (Higham and Maestripieri 2010; Higham *et al.* 2011b). During the mating season we collected standardized images of male faces, and rump and genital regions; we then measured the color and luminance of each area (Higham *et al.* 2013b). We also present mortality data on Cayo Santiago from a much wider period, including all deaths in the rhesus population between 1961 and 2005 (Hoffman *et al.* 2008). All work undertaken for the original papers and described in this review was performed according to ethical guidelines published by animal behavior and primatological societies, was approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico, and adhered to the legal requirements of Puerto Rico and the United States.

The Birth Season: Resting and Building Condition

Bercovitch (1992, 1997) suggested that a key element to male rhesus macaque reproductive success is the ability of males to build condition in the birth season, which then determines their ability to compete in endurance rivalry during the mating season. To do this, males should exhibit relatively low levels of potentially costly physiological primers such as testosterone, while conserving energy and gaining strength by maintaining positive energy balance. In a recent publication, we showed that indeed, during the birth season, all adult males showed relatively low androgen concentrations (Fig. 1), when compared to the period of reproductive competition. Mean (\pm SEM) male androgen values were: birth season (mean = 3324.3 ± 449.3 ng/g dry fecal weight); peak of the mating season (mean = 4464.5 ± 437.8 ng/g); last 3 mo of the mating season (mean = 2946.3 ± 261.4 ng/g) (Higham *et al.* 2013a). Although patterns were broadly similar for GCs, differences between the three periods were not significantly different (birth season, mean = 332.8 ± 29.0 ng/g; peak of the mating season, 468.0 ± 49.3 ng/g; last 3 mo of mating season, mean = 370.2 ± 32.7 ng/g) (Higham *et al.* 2013a). Our results are consistent with a range of data from other seasonally breeding primates, showing that androgen levels are typically reduced outside mating periods.

Older males showed particularly low androgen concentrations, with age negatively related to androgen output. Splitting the 15 birth season males into 2 subsets based on whether they are younger or older than the median male age in the dataset (14 yrs) shows that males >14 yrs had mean birth season androgen concentrations of 2330.8 ± 476.6 ng/g ($N = 7$), whereas males <14 yrs had mean birth season androgen levels of 3887.5 ± 508.2 ng/g ($N = 8$). A number of studies of humans and other anthropoid primates have shown significant age-related declines in androgen concentrations among males, with these typically linked to ideas of reproductive senescence, e.g., humans (Bribiescas 2006) and chacma baboon and gelada males (Beehner *et al.* 2009). A nonmutually exclusive explanation for our result could be that older males have more offspring in the group, given that mammalian fathers

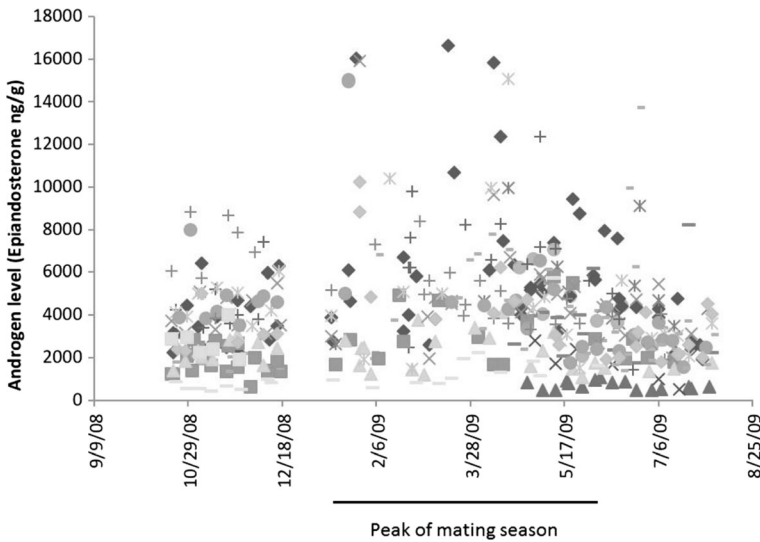


Fig. 1 Androgen concentrations over the course of a 10-mo period (October 2008–August 2009) for the rhesus macaque study males on Cayo Santiago (where each different symbol represents a different male). The approximate peak of the mating season is indicated. Androgen concentrations were significantly higher in the peak mating period than they were in the birth season. No significant differences were found between the birth period and the last 3 mo of the mating season (Higham *et al.* 2013a).

exhibiting nurturant paternal care typically show lower androgen levels (Wynne-Edwards 2001). It is unclear whether rhesus macaque males show such nurturant behaviors, although there is evidence for paternal kin recognition in this species (Widdig *et al.* 2001), and males do sometimes pick up and carry infants, often lip-smacking at them as they do so.

There were no significant relationships between male rank and androgen or glucocorticoid concentrations during the birth season (Higham *et al.* 2013a). High-ranking individuals did, however, spend more time feeding on high-energy monkey chow and less time traveling than low-ranking individuals (Higham *et al.* 2011b). High-ranking males thus took advantage of their status to rest and feed, building their physical condition. They were also less restless, a condition operationally defined as the number of behavioral transitions from one behavioral state to another (Higham *et al.* 2011b). Presumably as a consequence of these behavioral differences, higher ranked individuals had higher UCP concentrations across the birth season (Fig. 2a), indicative of better energetic condition and overall greater body fat (Girard-Buttoz *et al.* 2011). During the trapping period at the end of the birth season, higher ranked males also had higher BMIs (Higham *et al.* 2011b).

High-ranking rhesus macaque individuals often threaten and lunge at low-ranking individuals seemingly at random (Maestripieri 2007), and it has been suggested that such random attacks in primate species are beneficial to attackers because they cause physiological stress responses that damage the health and fertility of rivals (Miller 1997; Silk 2002). Such hostile acts may create anxiety, which has often been linked to fidgeting and restlessness in humans (Heerey and Kring 2007; Kavan *et al.* 2009; Mehrabian and Friedman 1986). Similar to our suggestion that increased behavioral transitions shown in lower ranked males in our data might be related to lower UCP

concentrations (Higham *et al.* 2011b), fidgeting and restlessness (Dunn and Kronenberger 2003) have been shown to be energetically costly, and have been linked to interindividual variation in weight among humans, and in the tendency of different individuals to gain and lose mass (Levine *et al.* 1999; Marra *et al.* 2007). As such, we have previously suggested that anxiety-related energy expenditure may reduce the ability of low-ranking males to improve their physical condition, and hence affect their ability to compete in endurance rivalry for females during the mating season (Higham *et al.* 2011b). Collectively, the results of our prior publications show that all males may benefit from reduced androgen levels outside of the period of mating competition, but that high-ranking individuals are best able to improve their condition in the birth season by monopolizing access to food resources, and by conserving energy by undertaking less energetically expensive behaviors.

The Mating Season I: The Costs of Success in Indirect Competition

Given the potential importance of indirect competition and endurance rivalry in rhesus macaque male mating competition, we used UCP concentrations to assess male energy balance and its relationships to mating activity. During the mating season, high-ranked individuals formed more consortships with females, with the top three ranked males all spending more than 30% of their time, and one of these males more than 50% of his time, in such consortships. In contrast, none of the bottom ranking 50% of males spent more than 10% of their time in consortships. These consortship periods were in turn associated with higher copulation rates (Higham *et al.* 2011b). Paternity analyses have shown that the use of this behavioral tactic is associated with substantial reproductive success (Berard *et al.* 1994). Mating activities constrain feeding: we found significant negative correlations between rates of copulation and rates of feeding (Higham *et al.* 2011b). The top 3 ranked males spent a mean 20.1% ($\pm 1.9\%$) of time feeding across the mating season, compared to a mean 28.7% ($\pm 1.4\%$) time feeding for the other 17 focal males. As a consequence, across the last 3 mo of the mating season high ranked males had lower UCP concentrations than lower ranked individuals — the reverse of the situation in the birth season (Fig. 2; Higham *et al.* 2011). These results suggest that higher ranked males, which were able to build their physical condition and fat reserves during the birth season, were able to use this good condition to undertake costly but successful strategies during the mating season. The differential success of males is directly related to their ability to undertake consortships over sustained periods of time in a process of endurance rivalry, as suggested by Bercovitch (1992, 1997).

The Mating Season II: The Costs of Periods of Direct Competition

As shown in Fig. 1 and discussed earlier, across all males, androgen concentrations were higher in the period of peak reproductive competition than they were in the birth season or in the last 3 mo of the mating season, but statistically significant differences between the three periods were not found for GCs (Higham *et al.* 2013a). Older males underwent a greater interseasonal rise from the birth season to the mating season. As a consequence, unlike in the birth season, there was no relationship between male age and androgen concentrations in the mating season (Higham *et al.* 2013a). As such, all males underwent increases in androgen levels to meet competitive needs during the

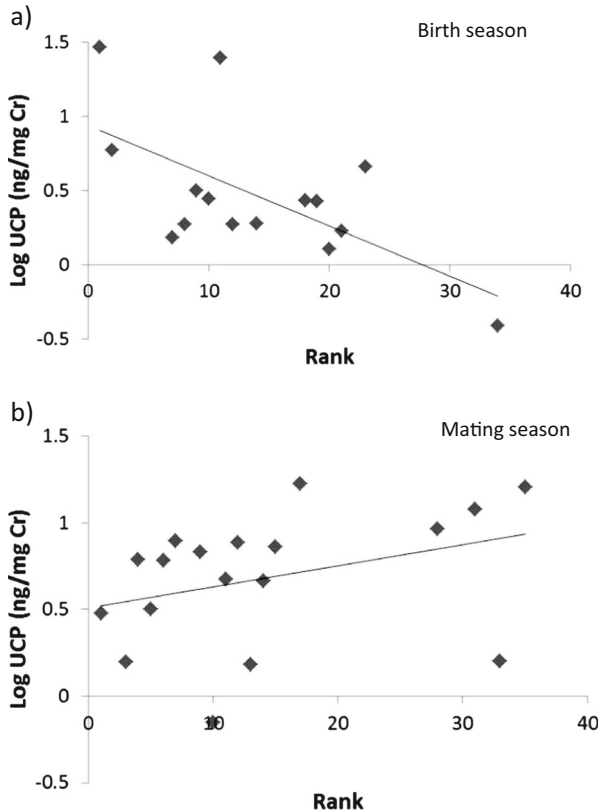


Fig. 2 (a) Rhesus macaque male urinary C-peptide (UCP) concentrations by dominance rank during the 2008 birth season on Cayo Santiago. There was a significant negative correlation, whereby higher ranked individuals had higher UCP concentrations. (b) In contrast, across the last 3 mo of the 2009 mating season, male UCP concentrations were significantly positively correlated with dominance rank, whereby higher ranked individuals had lower UCP concentrations (Higham *et al.* 2011b).

mating season. Similar findings have been reported in many other primate species, including in strepsirrhines, e.g., Verreaux's sifakas (*Propithecus verreauxii*: Fichtel *et al.* 2007; Kraus *et al.* 1999); platyrrhines, e.g., tufted capuchins (*Cebus apella nigrilus*: Lynch *et al.* 2002); and other catarrhines, e.g., Assamese macaques (*Macaca assamensis*: Ostner *et al.* 2011).

Rhesus males bear the hallmarks of reduced direct competition compared to many other Papionins. However, like all macaques, they are sexually dimorphic, and this suggests at least some degree of direct contest competition between males over females. In the Cayo Santiago rhesus population, during the past few years there have been several periods in which males have fought openly over dominance. When this occurs, it seems to take the form of agonistic coalitions, with multiple individuals attacking the same individual repeatedly. One such period occurred in 2009, during the last 3 mo of the mating season (Higham and Maestriperi 2010). What leads to such periods of social upheaval is still unclear, but at the time of the 2009 revolutionary coalitions the highest ranking individuals included some very old males and several young natal males, while there were many prime-aged males in the middle ranks. These prime males formed revolutionary coalitions and

ousted high-ranking individuals (Higham and Maestripieri 2010). During this period of direct contest competition over dominance, males showed many of the characteristic responses of male primates to direct competition. Although there were no relationships between rank and GC or androgen concentrations under conditions when dominance hierarchies were stable, higher ranked individuals exhibited significantly higher concentrations of GCs and androgens during periods of dominance instability (Higham *et al.* 2013a). Splitting males into just two rank categories (higher and lower, based on ranks at the start of the period of rank instability) showed that mean (\pm SEM) GC concentrations were 434.7 ± 37.5 ng/g for higher ranked males compared to 312.2 ± 45.0 ng/g for lower ranked males, while mean androgen concentrations were 3338.0 ± 260.6 ng/g for higher ranked males compared to 2593.7 ± 412.4 ng/g for lower ranked males (Higham *et al.* 2013a). There were also particularly high concentrations of both endocrine parameters for those males targeted by coalition members (Higham *et al.* 2013a). These hormonal changes were probably instrumental in the priming of males for contest competition (androgens) and in the mobilization of the necessary energy associated with this type of competition, given the role of GCs in increasing levels of blood sugar, and in aiding the metabolism of fat, protein, and carbohydrates. These types of changes in response to rank instability are similar to those seen in species that show rank instability and direct contest competition over dominance more consistently, such as chacma baboons (*Papio ursinus*: Bergman *et al.* 2005) and mandrills (Setchell *et al.* 2010b).

Sexually Selected Traits

In addition to measuring behavior and patterns of hormone excretion across the year, we also investigated potential sexually selected traits. The reproductive competition exhibited by rhesus males should select for traits related to indirect mechanisms such as endurance rivalry and sperm competition rather than for traits such as large body and canine size dimorphism. We attempted to measure relevant aspects of sperm morphology such as swimming speed and percentage motility through the collection of sperm in the field, but were unsuccessful. Other authors have had more success in measuring sperm in field conditions (Thomsen 2013), and such methods hold great promise for tackling this issue in the future.

In addition to sexually selected traits related to indirect male–male competition, species exhibiting indirect male–male competition should also be subject to stronger intersexual selection (mate choice) mechanisms than those species where direct male–male competition is the predominant means by which male mating success is determined. Intersexual selection in turn leads to the evolution of ornaments attractive to the opposite sex, rather than weapons with which to outcompete the same sex (Clutton-Brock and McAuliffe 2009). We measured one potentially sexually selected trait in our study males, facial coloration, which could potentially be related to either male–male competition (if it were a male social status signal), or to mate choice (if it were a signal to attract females), or to both. Unlike in those Papionin species exhibiting higher levels of male–male competition, reproductive skew, and sexual dimorphism, such as mandrills (Setchell and Wickings 2005), drills (Marty *et al.* 2009), and geladas (Bergman *et al.* 2009), we found no relationship between male coloration and dominance rank, nor between coloration and androgen concentrations (Higham *et al.* 2013b). The former of these two results has since been confirmed in a different data set (Dubuc *et al.* 2014b).

Instead, the available evidence suggests that male rhesus macaques may use coloration to attract females. First, females look longer at face images of experimentally reddened males, with this increased looking time inferred as a preference for such faces (Waitt *et al.* 2003). Second, although we found no relationships between overall mating activity and male coloration (Higham *et al.* 2013b), a new study using a data set with improved measures of female proceptivity has found that females exhibit more proceptive sexual behaviors toward males of darker facial color (Dubuc *et al.* 2014b). In a system in which females exert a high degree of direct mate choice, and where low rates of direct male–male competition make it difficult to infer male quality from rank, males may evolve ornaments that function primarily to attract females rather than to indicate social status (Dubuc *et al.* 2013; Higham *et al.* 2012, 2013b). Consistent with a high degree of scope for female mate choice in rhesus macaques, females in this study population actively solicit males independently of male dominance rank, including low-ranking peripheral males (Berard *et al.* 1994).

Life History

Our previously published data show that mating competition among males involves many aspects of their behavior and physiology. Ultimately, however, perhaps the most important question is how these short-term costs affect mortality over time. Luckily, the Cayo Santiago population is perfect to address this question, as data on mortality has been recorded for decades. Given the physiological and behavioral consequences of male mating competition, in what way might these lead to survival costs? Using 45 years of data on 922 deaths in both males and females, Hoffman *et al.* (2008) showed that female mortality is high during the birth season and low in the mating season, whereas male mortality is low during the birth season and high during the mating season (Fig. 3). As such, there are sex-specific costs of reproduction in this species. Given the male-biased mortality in the mating season, we suggest that the costs of male–male competition outlined in the present review are likely to be linked to the high male mortality seen at this time. Survival costs of reproductive competition have been seen in other primate species such as mouse lemurs (Kraus *et al.* 2008), as well as other mammals such as ground squirrels (Neuhaus and Pelletier 2001).

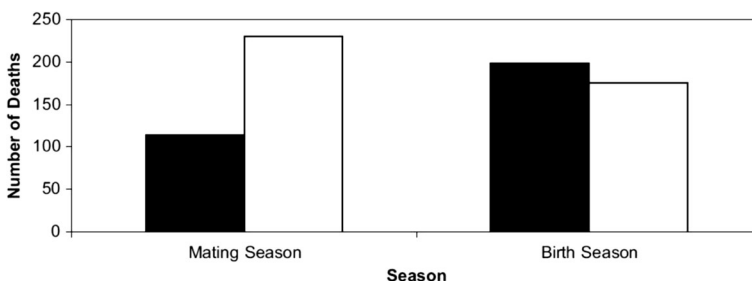


Fig. 3 Number of female (black bars) and male (white bars) rhesus macaque deaths on Cayo Santiago between 1961 and 2005 (Hoffman *et al.* 2008).

Conclusions and Discussion

Our studies have been able to identify a number of behavioral and physiological costs of reproductive competition in male rhesus macaques on Cayo Santiago. We here set these into the context of rhesus macaque reproductive strategies, and how these compare with those of other Papionins.

Collectively, our results are consistent with a species in which indirect male–male competition is important. Bercovitch (1992, 1997) suggested that in rhesus macaques, the birth season is important for male reproductive strategies, because it is in this period that males build their body condition by maintaining positive energy balance, and that the relative ability of males to improve their condition at this time will directly influence their ability to undertake successful but energetically costly strategies during the mating season. Our studies provide physiological, morphological, and behavioral support for Bercovitch's ideas, with high-ranking males building condition during the birth season, and these same males undertaking consortships with high rates of copulations, and finishing the mating season in the worst nutritional condition. Our data provide an example of how endurance rivalry can function in nonhuman primates, and how this process can link the birth season to the mating season. They also reveal that access to food and reduced energy expenditure during the birth season may be some of the key reproductive advantages to high rank for males in this species.

One of the consequences of a decreased role for direct competition is lower sexual dimorphism in body size and weaponry, and this is indeed found in rhesus compared to most Papionins (Plavcan 2004). In addition, we expect that reduced direct competition should obviate the need for signals such as colors to act as badges of status. At the same time lower sexual dimorphism and lower reproductive skew lead to an increased role for female mate choice, making male signals that are attractive to females more likely to evolve.

Despite a relatively reduced role for direct competition, e.g., little contest competition over dominance (Manson 1995), we nonetheless still found evidence for the effects of direct competition. Male androgen concentrations were higher during the mating season than the birth season, though this may be necessary for instigation of sexual behavior. We documented a clearer signal of the effects of direct competition during periods of rank instability, when males fought more openly over dominance, with this reflected in rank-related androgen and GC excretion patterns. As a sexually dimorphic multimale multifemale group-living promiscuous primate, rhesus clearly have some element of direct male–male competition, even if this is reduced compared to many other species in their clade.

In sum, rhesus macaques provide an interesting counterpoint to the typical story of the primate Papionin male, in which contest competition over dominance leads to strong sexual dimorphism and marked reproductive skew. This is not to say that rhesus macaques do not experience strong sexual selection pressures—the relatively large testis size of males is a clear indication that they do. However, selection via indirect competition has acted to increase the expression of traits related to such mechanisms. The costs of male–male competition are therefore somewhat different in species at the rhesus macaque end of the continuum of direct to indirect male–male competition on which Papionin species sit.

Future Directions

One poorly documented aspect of male mating competition in rhesus macaques is sperm competition. Given the large testis size in this species, and the high number of copulations undertaken by males during the mating season, we predict sperm competition will be highly important. Given the demonstrable costs of male sperm production, e.g., adders (Olsson *et al.* 1997), the large amount of sperm apparently produced seems likely to bring significant costs to males. As noted previously, studies have managed to collect and measure sperm in the field, but our attempts to do so in this rhesus population have not been successful, and previous studies on Cayo Santiago have been limited to observations of sperm plugs (Danzey *et al.* 2009). However, this remains an exciting potential avenue of future research.

Given the relatively large scope for direct female mate choice in this species, more studies of the basis on which females choose mates would seem potentially fruitful. Prior studies have suggested that rhesus macaque females may prefer novel males, but the evidence is weak at best (Manson 1995). This may be because females prefer novel, peripheral males when they happen to be of good quality, and not when those males happen not to be of particularly good quality. This leads to questions about what traits females might be looking for in males. An experimental study (Waite *et al.* 2003), and a recent observational study (Dubuc *et al.* 2014b) have indicated that females prefer males with redder/darker faces, but what color variation may indicate to females is unknown, given that it correlates neither with rank nor with testosterone levels in this population. To our knowledge there has only been one prior study of major histocompatibility complex (MHC) variation as it relates to overall reproductive success in rhesus macaques. This found that males that were heterozygous at the MHC Class II complex had higher reproductive success (Saueremann *et al.* 2001). Previous studies of other Papionins have shown that males and females may select on the basis of complementary or specific MHC types, or overall MHC diversity (Setchell and Huchard 2010). Of the Papionins studied so far, rhesus macaques may perhaps have greater scope for direct female choice than much more markedly sexually dimorphic species such as mandrills. Though there is evidence that mandrills do indeed show MHC-related mate choices (Setchell *et al.* 2010a), alpha males nonetheless typically sire *ca.* 70% of infants (Charpentier *et al.* 2005; Setchell *et al.* 2005). Though this varies from as little as 33% to as much as 100% (Setchell *et al.* 2005), even this lower figure is higher than values usually obtained by rhesus macaque alpha males. Rhesus macaques, with a much lower proportion of variance explained by dominance rank, have greater scope for other variables to explain variance in male reproductive success.

Other parameters missing from our studies so far are physiological measures of health and immune function. In species with greater levels of direct male–male competition, there have been numerous accounts of the costs of direct competition, such as the maiming of digits and large open gashes and wounds, e.g., mandrills (Setchell and Wickings 2005). These are likely to lead to increased likelihood of infection, making the links among behavior, health, and mortality clear (Archie *et al.* 2012). However, in a dynamic of increased indirect competition, these connections may be less obvious. Physiological consequences of exertion in indirect processes such as

endurance rivalry and sperm competition are unlikely to lead to the obvious wounds and injuries that can be easily linked to infection and disease. As such, physiological measures of immune activation and health (see Prall and Muehlenbein 2014) are likely to be particularly important for understanding the links between behavioral strategies and patterns of mortality in Cayo Santiago males. Reliable and informative noninvasive measures of immune function have not traditionally been available, but new studies seek to obtain such measures from noninvasive sources such as saliva (Higham *et al.* 2010), and we are currently validating measures from urine and feces. What are the consequences of energetic stress and high androgen concentrations for male immune responsiveness and for the vulnerability of males to infectious diseases? The answers to such questions will enable us to fill the missing pieces of the puzzle, and link behavior and physiology to health outcomes, and ultimately to mortality.

Acknowledgments We thank all of the researchers, students, and staff at the University of Chicago, the Caribbean Primate Research Center, and the German Primate Center who contributed to the research reviewed in this article, as well as Constance Dubuc and Antje Engelhardt for discussion. We thank Alex Georgiev and Melissa Emery Thompson for inviting us to speak at the 2013 AAPA symposium, and to contribute to this special issue. We are also grateful to Melissa Emery Thompson and three anonymous reviewers for helpful comments on previous versions of this manuscript. This research was supported by NIH grant R21-AG029862 to D. Maestripieri, and by an IPS research grant to J. P. Higham. This publication was made possible by grant number CM-5-P40RR003640 from the NIH National Center for Research Resources (NCRR) to the Caribbean Primate Research Center of the University of Puerto Rico. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of NCRR or NIH.

References

- Andersson, M. (1994). *Sexual selection*. Princeton: Princeton University Press.
- Archie, E. A., Altmann, J., & Alberts, S. C. (2012). Social status predicts wound healing in wild baboons. *Proceedings of the National Academy of Sciences USA*, *109*, 9017–9022.
- Beehner, J. C., Geschiere, L., Cheney, D. L., Seyfarth, R. M., & Altmann, J. (2009). Fecal testosterone related to age and life-history stages in male baboons and geladas. *Hormones and Behavior*, *56*, 472–480.
- Berard, J. D., Nürnberg, P., Epplen, J. T., & Schmidtke, J. (1994). Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour*, *129*, 177–201.
- Bercovitch, F. B. (1992). Estradiol concentrations, fat deposits, and reproductive strategies in male rhesus macaques. *Hormones and Behavior*, *26*, 272–282.
- Bercovitch, F. B. (1997). Reproductive strategies of rhesus macaques. *Primates*, *38*, 247–263.
- Bergman, T. J., Beehner, J. C., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2005). Correlates of stress in free-ranging male chacma baboons. *Animal Behaviour*, *70*, 703–713.
- Bergman, T., Ho, L., & Beehner, J. (2009). Chest color and social status in male geladas (*Theropithecus gelada*). *International Journal of Primatology*, *30*, 791–806.
- Bribiescas, R. G. (2006). *Men: Evolutionary and life history*. Cambridge, MA: Harvard University Press.
- Charpentier, M., Peignot, P., Hossaert-McKey, M., Gimenez, O., Setchell, J. M., & Wickings, E. J. (2005). Constraints on control: Factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behavioral Ecology*, *16*, 614–623.
- Clutton-Brock, T., & McAuliffe, K. (2009). Female mate choice in mammals. *The Quarterly Review of Biology*, *84*, 3–27.
- Danzon, J., Gutierrez, V., Pampush, J., & Campbell, B. (2009). Factors affecting the distribution of copulatory plugs in rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. *Folia Primatologica*, *80*, 264–274.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.
- Dubuc, C., Allen, W., Maestripieri, D., & Higham, J. P. (2014a). Is male rhesus macaque red color ornamentation attractive to females? *Behavioral Ecology and Sociobiology*, *68*, 1215–1224.

- Dubuc, C., Higham, J. P., & Engelhardt, A. (2013). Towards a theoretical framework for understanding the variation in sexually-selected traits among multimale-multifemale anthropoid primates. *American Journal of Physical Anthropology*, *150*, 115–116.
- Dubuc, C., Muniz, L., Heistermann, M., Engelhardt, A., & Widdig, A. (2011). Testing the priority-of-access model in a seasonally breeding species. *Behavioral Ecology and Sociobiology*, *65*, 1615–1627.
- Dubuc, C., Ruiz Lambides, A., & Widdig, A. (2014b). Variance in male lifetime reproductive success and estimation of the degree of polygyny in a primate. *Behavioral Ecology*, *25*, 878–889.
- Dunn, D. W., & Kronenberger, W. G. (2003). Attention-deficit/hyperactivity disorder in children and adolescents. *Neurologic Clinics*, *21*, 933–940.
- Fichtel, C., Kraus, C., Ganswindt, A., & Heistermann, M. (2007). Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas (*Propithecus verreauxi*). *Hormones and Behavior*, *51*, 640–648.
- Girard-Buttoz, C., Higham, J. P., Heistermann, M., Wedegärtner, S., Maestriperi, D., & Engelhardt, A. (2011). Urinary C-peptide measurement as a marker of nutritional status in macaques. *PLoS One*, *6*, e18042.
- Gogarten, J. F., & Koenig, A. (2013). Reproductive seasonality is a poor predictor of receptive synchrony and male reproductive skew among nonhuman primates. *Behavioral Ecology and Sociobiology*, *67*, 123–134.
- Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight, body weight and breeding system in primates. *Nature*, *293*, 55–57.
- Harcourt, A. H., Purvis, A., & Liles, L. (1995). Sperm competition: Mating system, not breeding season, affects testes size of primates. *Functional Ecology*, *9*, 468–476.
- Heerey, E. A., & Kring, A. M. (2007). Interpersonal consequences of social anxiety. *Journal of Abnormal Psychology*, *116*, 125–134.
- Higham, J. P., Girard-Buttoz, C., Engelhardt, A., & Heistermann, M. (2011a). Urinary C-peptide of insulin as a non-invasive marker of nutritional status: Some practicalities. *PLoS One*, *6*, e22398.
- Higham, J. P., Heistermann, M., & Maestriperi, D. (2011b). The energetics of male-male endurance rivalry in rhesus macaques. *Animal Behaviour*, *81*, 1001–1007.
- Higham, J. P., Heistermann, M., & Maestriperi, D. (2013a). The endocrinology of male rhesus macaque social and reproductive status: A test of the challenge and social stress hypotheses. *Behavioral Ecology and Sociobiology*, *67*, 19–30.
- Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D., & Engelhardt, A. (2012). Sexual signaling in the crested macaque and the evolution of primate fertility signals. *BMC Evolutionary Biology*, *12*, 89.
- Higham, J. P., & Maestriperi, D. (2010). Revolutionary coalitions in male rhesus macaques. *Behaviour*, *147*, 1889–1908.
- Higham, J. P., Pfeifferle, D., Heistermann, M., Maestriperi, D., & Stevens, M. (2013b). Signaling in multiple modalities in male rhesus macaques: Barks and sex skin coloration in relation to androgen levels, social status and mating behavior. *Behavioral Ecology and Sociobiology*, *67*, 1457–1469.
- Higham, J. P., Vitale, A. B., Mas-Rivera, A., Ayala, J. E., & Maestriperi, D. (2010). Measuring salivary analytes from free-ranging monkeys. *Physiology & Behavior*, *101*, 601–607.
- Hoffman, C. L., Higham, J. P., Mas-Rivera, A., Ayala, J. E., & Maestriperi, D. (2010). Terminal investment and senescence in rhesus macaques on Cayo Santiago. *Behavioral Ecology*, *21*, 972–978.
- Hoffman, C. L., Ruiz-Lambides, A. V., Davila, E., Maldonado, E., Gerald, M. S., & Maestriperi, D. (2008). Sex differences in survival costs of reproduction in a promiscuous primate. *Behavioral Ecology & Sociobiology*, *62*, 1711–1718.
- Kavan, M. G., Elsasser, G. N., & Barone, E. J. (2009). Generalized anxiety disorder: practical assessment and management. *American Family Physician*, *79*, 785–791.
- Kraus, C., Eberle, M., & Kappeler, P. M. (2008). The costs of risky male behaviour: Sex differences in seasonal survival in a small sexually monomorphic primate. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*, 1635–1644.
- Kraus, C., Heistermann, M., & Kappeler, P. M. (1999). Physiological suppression of sexual function of subordinate males: A subtle form of intrasexual competition among male sifakas (*Propithecus verreauxii*)? *Physiology and Behavior*, *66*, 855–861.
- Kutsukake, N., & Nunn, C. L. (2006). Comparative tests of reproductive skew in male primates: The roles of demographic factors and incomplete control. *Behavioral Ecology and Sociobiology*, *60*, 695–706.
- Levine, J. A., Eberhardt, N. L., & Jensen, M. D. (1999). Role of nonexercise activity thermogenesis in resistance to fat gain in humans. *Science*, *283*, 212–214.
- Lynch, J. W., Ziegler, T. E., & Strier, K. B. (2002). Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus apella nigrilus*. *Hormones and Behavior*, *41*, 275–287.

- Maestripieri, D. (2007). *Macchiavellian intelligence*. Chicago: The University of Chicago Press.
- Manson, J. H. (1995). Do female rhesus macaques choose novel males? *American Journal of Primatology*, *37*, 285–296.
- Marra, M., Pasanisi, F., Montagnese, C., De Filippo, E., De Caprio, C., De Magistris, L., & Contaldo, F. (2007). BMR variability in women of different weight. *Clinical Nutrition*, *26*, 567–572.
- Marty, J. S., Higham, J. P., Gadsby, E. L., & Ross, C. (2009). Dominance, coloration and social and sexual behavior in male drills (*Mandrillus leucophaeus*). *International Journal of Primatology*, *30*, 807–823.
- Mehrabian, A., & Friedman, S. L. (1986). An analysis of fidgeting and association individual differences. *Journal of Personality*, *54*, 406–429.
- Miller, G. F. (1997). Protean primates: The evolution of adaptive unpredictability in competition and courtship. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian intelligence II: extensions and evaluations* (pp. 312–340). Cambridge: Cambridge University Press.
- Muehlenbein, M. P., Campbell, B. C., & Murchison, M. A. (2002). Morphological and hormonal parameters in two species of macaques: Impact of seasonal breeding. *American Journal of Physical Anthropology*, *117*, 218–227.
- Neuhaus, P., & Pelletier, N. (2001). Mortality in relation to season, age, sex and reproduction in Columbian ground squirrels (*Spermophilus columbianus*). *Canadian Journal of Zoology*, *79*, 465–470.
- Olsson, M., Madsen, T., & Shine, R. (1997). Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proceedings of the Royal Society of London B: Biological Sciences*, *264*, 455–459.
- Ostner, J., Heistermann, M., & Schülke, O. (2011). Male competition and its hormonal correlates in wild Assamese macaques (*Macaca assamensis*). *Hormones and Behavior*, *59*, 105–113.
- Ostner, J., Nunn, C. L., & Schülke, O. (2008). Female reproductive synchrony predicts skewed paternity across primates. *Behavioral Ecology and Sociobiology*, *19*, 1150–1158.
- Plavcan, J. M. (1997). Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, *103*, 37–68.
- Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology*, *44*, 25–53.
- Plavcan, J. M. (2004). Sexual selection, measures of sexual selection, and sexual dimorphism in primates. In P. M. Kappeler & C. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives*. New York: Cambridge University Press.
- Plavcan, J. M. (2011). Understanding dimorphism as a function of changes in male and female traits. *Evolutionary Anthropology*, *20*, 143–155.
- Plavcan, J. M., & van Schaik, C. P. (1992). Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, *87*, 461–477.
- Prall, S. P., & Muehlenbein, M. P. (2014). Testosterone and immune function in primates: a brief summary with methodological considerations. *International Journal of Primatology*. doi:10.1007/s10764-014-9752-x.
- Rawlins, R. G., & Kessler, M. J. (Eds.). (1986). *The Cayo Santiago macaques: History, behavior & biology*. Albany: SUNY Press.
- Saueremann, U., Nürnberg, P., Bercovitch, F. B., Berard, J. D., Trefilov, A., Widdig, A., Kessler, M., Schmidtko, J., & Krawczak, M. (2001). Increased reproductive success of MHC class II heterozygous males among free-ranging rhesus macaques. *Human Genetics*, *108*, 249–254.
- Setchell, J. M., & Huchard, E. (2010). The hidden benefits of sex: Evidence for MHC-associated mate choice in primate societies. *BioEssays*, *32*, 940–948.
- Setchell, J. M., Charpentier, M., & Wickings, E. J. (2005). Mate-guarding and paternity in mandrills (*Mandrillus sphinx*): Factors influencing monopolization of females by the alpha male. *Animal Behaviour*, *70*, 1105–1120.
- Setchell, J. M., Charpentier, M. J. E., Abbott, K. M., Wickings, E. J., & Knapp, L. A. (2010a). Opposites attract: MHC-associated mate choice in a polygynous primate. *Journal of Evolutionary Biology*, *23*, 136–148.
- Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2010b). Stress, social behaviour and secondary sexual traits in a male primate. *Hormones and Behavior*, *58*, 720–728.
- Setchell, J. M., & Wickings, E. J. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology*, *111*, 25–50.
- Silk, J. B. (2002). Practice random acts of aggression and senseless acts of intimidation: the logic of status contests in social groups. *Evolutionary Anthropology*, *11*, 221–225.
- Thomsen, R. (2013). Non-invasive collection and analysis of semen in wild macaques. *Primates*. doi:10.1007/s10329-013-0393-z.
- van Noordwijk, M. A., & van Schaik, C. P. (2004). Sexual selection and the careers of primate males: Paternity concentration, dominance acquisition tactics and transfer decisions. In P. M. Kappeler & C. P.

- van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 208–229). Cambridge, U.K.: Cambridge University Press.
- Waitt, C., Little, A. C., Wolfensohn, S., Honess, P., Brown, A. P., Buchanan-Smith, H. M., & Perrett, D. I. (2003). Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, S144–S146.
- Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences of the USA*, *98*, 13769–13773.
- Wynne-Edwards, K. E. (2001). Hormonal changes in mammalian fathers. *Hormones and Behavior*, *40*, 139–145.