Body size and canine size do not confer a competitive advantage in male rhesus macaques

Abstract

Male armaments are hypothesized to have evolved under intra-sexual selection. Such traits may function as signals, weapons, or both, in male-male mating competition. Primate sexually dimorphic canine teeth and body size are two potentially weaponized traits whose function as a signal and/or weapon remains unclear, largely due to the difficulty of collecting detailed measurements of morphology on large free-ranging mammals. Rhesus macaques (*Macaca mulatta)* are an interesting study system in which to investigate how such traits function because they experience relatively low levels of direct male-male mating competition compared to other members of their subfamily. Furthermore, male dominance rank is largely based on a queuing-system rather than on the outcome of inter-male aggressive encounters. We leveraged a novel dataset of behavioral observations and morphometric data from free-ranging rhesus macaques to investigate the function of sexually dimorphic canine teeth and body mass as weapons and/or signals. We tested whether canine height or body mass was correlated with dominance rank, whether similarity in any of these factors influenced the occurrence or outcome of agonistic interactions between male-male dyads, and whether either of these traits predicted the likelihood of winning an agonistic interaction. Neither canine height nor body mass was related to dominance rank. Similarity in dominance rank, but not in morphology, predicted the occurrence of agonism between dyads. Agonistic encounters between males more similar in dominance rank were more likely to be characterized by aggression rather than submission. Dominance rank, but not canine height or body mass, predicted the likelihood of winning an agonistic interaction. Our results suggest that canine height and body mass do not confer a strong competitive advantage in male rhesus macaques and add to a growing body of evidence indicating that weaponized traits do not always seem to function either in fights or as signals in male-male combat.

Highlights

- Male armaments are hypothesized to have evolved under intra-sexual selection.
- Armaments may function as signals, weapons, or both, in male-male contests.
- Male primate canine teeth and body mass are traits that may influence contest outcomes.
- We tested whether these traits conferred an advantage in male-male combat.
- We found no evidence that these traits conferred a competitive advantage.

Keywords: sexual selection, mating competition, sexual dimorphism, armament, rhesus macaque

Introduction

Sexual selection explains the evolution of exaggerated traits across the animal kingdom via intersexual selection (mate choice), intrasexual selection (mate competition), or both (Darwin 1871; Andersson 1994; Hunt et al. 2009). Generally, intrasexual selection produces armaments that enhance fighting ability and make individuals better at competing with members of their own sex for mating opportunities (Emlen 2008; McCullough et al. 2016). Armaments used in direct male-male contest competition, such as large male body size and weaponized traits, are found across many vertebrates and arthropods (e.g., cervid antlers (Clutton-Brock et al. 1979; Hoem et al. 2007), bovid horns (Lundrigan 1996; Preston et al. 2003), crustacean claws (Caldwell and Dingle 1979; Jennions and Backwell 1996), and beetle horns (Emlen et al. 2005), among others (reviewed in Emlen (2008), Rico-Guevara and Hurme (2019)). Armament function exists on a continuum, from traits solely used as weapons, to traits that act as both signals and weapons, and finally to traits that are only used as signals (McCullough et al. 2016). Armaments are considered weapons when they are used in fights to intimidate or injure rivals, and signals when they function as indicators of fighting ability or strength to intimidate rivals and/or to attract mates (Emlen 2008; McCullough et al. 2016). This continuum framework can be used to test predictions about selection on armament form in relation to function. Specifically, in contexts in which traits primarily function as weapons, theory predicts that they should be more robust, and where traits function as signals, theory predicts that they should be more elaborate (McCullough et al. 2016). There is substantial evidence that armaments are used in fights; in many cases, males with larger weapons are more likely to win contests (e.g., monkey beetle *Heterochelus chiragricus* hind femur size (Rink et al. 2019), giraffe weevil *Trachelophorus giraffa* body length (Painting and Holwell 2014), red deer *Cervus elephas* antlers (Clutton-Brock et al. 1979), elephant seal *Mirounga angustirostris* body size (Haley et al. 1994)).

In contexts in which armaments function as signals, individuals may use trait size or form to assess a rival's competitive ability relative to their own prior to engaging in a costly fight (Arnott and Elwood 2009). Game theory predicts that animals equally-matched in weaponry are more likely to fight, and where there is a large asymmetry in weaponry animals should avoid physical fights (Smith 1979). This prediction is generally supported, with some exceptions. For example, size differences predict the likelihood of agonism in caribou *Rangifer tarandus* (Barrette and Vandal 1990), leaf-footed cactus bugs *Narnia femorata* (Nolen et al. 2017), and Magellanic penguins *Spheniscus magellanicus* (but only before egg-laying) (Renison et al. 2002), as well as the duration of agonistic interactions in fiddler crabs *Uca annulipes* (Jennions and Backwell 1996) and species of stalk-eyed flies (Diopsidae) (Panhuis and Wilkinson 1999), suggesting that these traits function as signals. However, body size and weapon size do not always influence fighting behavior (e.g., fallow deer *Dama dama* (Jennings et al. 2006), male snow skinks *Niveoscincus microlepitodus* (Olsson and Shine 2000)). These examples, among others, suggest that males may use a range of assessment strategies when deciding whether or not to engage in a fight (e.g., (Chapin et al. 2019), such that large male body size and weaponry do not always function as signals in male-male competition. Additional work is necessary to uncover the function of male weaponry across taxa and social/mating systems.

The evolution and function of male weaponry is predicted to relate to mating system variation, particularly male competitive regimes (Clutton-Brock 2017). The degree to which males compete directly (through fights) versus indirectly (competition without physical fighting, e.g., through endurance rivalry, in which males exclude other males from mating through prolonged periods of mate-guarding and mating (Andersson 1994) or sperm competition (Parker 1970)) is influenced by group size and mating system, particularly the degree to which males can monopolize access to fertile females (van Noordwijk and van Schaik 2004; Ostner et al. 2008). In systems where high-ranking males are able to gain a large share of the paternity in a group, males are likely to contest dominance (van Noordwijk and van Schaik 2004). In such systems, males with the largest weapons or largest body sizes are best able to attain high rank and high reproductive success (Andersson 1994; Clutton-Brock 2017). However, where high-ranking males cannot effectively monopolize paternity, and reproductive skew based on dominance rank is relatively low, such as in multi-male multi-female mating systems where females are highly synchronous in their fertile phases, or in large groups, rank is less likely to be contested (van Noordwijk and van Schaik 2004). Dominance rank acquisition through succession has been observed in wild populations of spotted hyenas *Crocuta crocuta* (East and Hofer 2001) and Kinda baboons *Papio kindae* (Petersdorf et al. 2019), as well as in provisioned populations of Japanese macaques *Macaca fuscata* (Yamagiwa and Hill 1998), and rhesus macaques *Macaca mulatta* (Manson 1995; Berard 1999). In these populations, males acquire rank by queuing such that male rank is a function of group tenure length rather than competitive ability (van Noordwijk and van Schaik 2004). Where males obtain dominance rank by queuing, weaponry need not be correlated with dominance rank and direct male-male competition may be a weaker selection pressure overall. Similarly, in multi-male multi-female mating systems with high degrees of female synchrony, males are more likely to compete through sperm competition or endurance rivalry rather than through fights, and weaponry is less likely to mitigate male-male conflict or to influence reproductive success (Parker 1970; Andersson 1994). These predictions have rarely been tested, particularly in taxa with reduced direct male-male competition, and less exaggerated armaments.

Two understudied traits that might influence the outcome of contests are sexually dimorphic canine teeth and body mass in primates (Plavcan and van Schaik 1992; Plavcan and van Schaik 1997a). Although many factors may produce sexual dimorphism in body size, there is evidence that, in primates, large male body size may have evolved under intrasexual selection (Plavcan and van Schaik 1997a). Across primate species, the level of sexual dimorphism in these traits correlates with the likelihood and intensity of fights between males (Plavcan and van Schaik 1992; Plavcan and van Schaik 1997a), yet the function of canine teeth and body size as signals and/or weapons is relatively unknown. To date there is only one published study on body size and agonism in male-male primate dyads, which showed that aspects of mountain gorilla *Gorilla beringei* body size influence male-male aggressive interactions (Wright et al. 2019).

Rhesus macaque males are a particularly interesting test case in which to investigate the function of sexually dimorphic canine teeth and body size because they exhibit a competitive regime characterized by reduced direct competition, such that males compete less through physical fights, when compared to other closely related species in their tribe (Papionini) (Higham and Maestripieri 2014). Rhesus macaques have a polygynandrous mating system and females are highly synchronous in their fertile phases (Melnick and Pearl 2008; Dubuc et al. 2011). High-ranking males are not able to monopolize paternity, leading to lower than predicted reproductive skew based on individual dominance rank compared with other closely-related species from their subfamily (Dubuc et al. 2011; Dubuc, Ruiz-Lambides, et al. 2014). Males usually queue for dominance rank; they enter groups at the bottom of the hierarchy and their rank increases with group tenure length such that dominance ranks calculated based on agonistic interactions correlate with residency length (Manson 1995; Berard 1999). Direct contests over rank may occur, but are rare (Higham and Maestripieri 2010; Georgiev et al. 2016). As expected in multi-male multi-female groups where males cannot monopolize paternity, males compete indirectly through sperm competition and endurance rivalry; they exhibit large testis volumes for their body size (Sade 1964; Bercovitch and Rodriguez 1993) and invest in building fat and energy reserves (Bercovitch 1992; Bercovitch 1997; Higham et al. 2011; Higham and Maestripieri 2014).

At the same time, however, rhesus macaques are also moderately sexually dimorphic in body mass (male mean divided by female mean: 1.31) and canine height (male mean divided by female mean: 2.07) (Plavcan and van Schaik 1997b). These levels of sexual dimorphism indicate some investment in direct competition, but these traits do not predict short-term reproductive success or average annual fecundity, nor do they correlate with ordinal dominance rank

(Bercovitch and Nürnberg 1996; Kimock et al. 2019). Interestingly, although male facial coloration is primarily selected through female mate choice, such that females attend to variation in male facial coloration (Dubuc et al. 2016), females mate preferentially with males with darker faces (Dubuc, Allen, et al. 2014), and males with both high dominance rank and darker facial coloration have higher reproductive success (Dubuc, Winters, et al. 2014), there is also some evidence to suggest that facial coloration mediates male-male agonistic interactions (Petersdorf et al. 2017). This mix of traits suggests that direct male-male contest competition may play a minor role in influencing the evolution of male rhesus macaque traits relative to indirect competition or female mate choice.

Direct tests of hypotheses about the assumed function of primate sexually dimorphic canine teeth and body mass are relatively rare because, in wild populations, it is difficult to collect good measurements (but see Wright et al. (2019)), and in captive populations it is generally not possible to collect naturalistic observations of agonistic behavior because animals that fight are often kept in separate enclosures. Here, we leverage a unique dataset of behavioral and morphometric data collected from free-ranging rhesus macaques to investigate whether sexually dimorphic canine teeth and body size function as weapons, signals, or both. First, we evaluated the relationships between **morphometrics and dominance rank (1).** Next, we assessed whether these traits function as signals **(2)** by determining if differences in canine height, body mass, and/or dominance rank predict the **occurrence of dyadic agonistic interactions** between males. Finally, we tested whether canine teeth and body size function as weapons **(3)** by evaluating their role in **contact aggression** specifically **(3.1)** and determining if differences in canine height and body mass predict the **outcome of agonistic interactions** generally, after controlling for dominance rank **(3.2)**. Given the fact that rhesus macaques are neither monomorphic, nor strongly dimorphic, and that the strength of male competition is only moderate in rhesus macaques, but that nonetheless males occasionally do fight, we made a series of alternative predictions. We predicted that morphometrics **(Pla)** might or **(P1b)** might not correlate with dominance rank, that differences in canine height, body mass, and/or dominance rank **(P2a)** might or **(P2b)** might not influence the occurrence of dyadic agonistic interactions between males, and that canine height and body mass might **(P3.1a)** or might not **(P3.1b)** influence the outcome of contact aggression and might **(P3.2a)** or might not **(P3.2b)** predict agonistic interactions more generally.

Material and Methods

Field site and subjects

This study was conducted on the free-ranging rhesus macaque population from Cayo Santiago, a small island located off the eastern coast of Puerto Rico. In 1938, 409 rhesus macaques were brought to the island for research purposes, and since then, the population has grown to over 1,800 animals (Kessler and Rawlins 2016). The Caribbean Primate Research Center (CPRC) monitors the population and maintains detailed long-term demographic (since 1958) and genetic parentage (since 1985) databases (Kessler and Rawlins 2016). The CPRC also provisions the macaques with commercial monkey chow and water. Although the rhesus macaques are not native, they form naturally occurring social groups and are not inbred (Widdig et al. 2017). We aggregated behavioral data and morphometric data on a subset of males ages six years old and above from three social groups (F, R, and V). Although male body mass growth is generally incomplete until about age seven, we chose to include males ages six and above because male canine teeth are fully erupted by age six (Wang 2012), most males disperse from their natal groups between the ages of four and six (Drickamer and Vessey 1973), and males are able to sire offspring from age five (Dubuc, Ruiz-Lambides, et al. 2014). As such, even though six-year-olds are not yet fully mature, they are mature enough to be competing for mating opportunities. At the time data for this study were collected, group F contained 61 adult males and 80 adult females, group R contained 61 adult males and 70 adult females, and group V contained 51 adult males and 42 adult females. Some of these males appeared in multiple groups over the course of the year; there were 155 unique males across all three groups.

Behavioral data

Trained field assistants conducted ten-minute continuous focal follows and recorded ad-lib agonistic interactions in the three study groups for a separate, unrelated project. Group F data were collected between late January and mid-October 2016, Group R data were collected between late February and mid-October 2016, and Group V data were collected between early February and mid-October 2016. Field assistants recorded the following behaviors: contact aggression (bite, hit, push, grab), non-contact aggression (lunge, charge, chase), threat (open mouth threat, stare threat, slap, head bob, huh!/bark), displacement, avoid, submit (submissive present, cower/lean), submit/threat, and fear grimace. Aggressive behaviors include contact aggression, non-contact aggression, threat, and displacement; while avoid, submit, and fear grimace are submissive behaviors. Submit/threat was recorded in the ad-lib data when both behaviors were observed simultaneously and therefore cannot be categorized as aggression or submission. Observers recorded the IDs of both partners in the interaction, along with the direction of the behavior.

Dominance rank

Dominance ranks were calculated within social groups using pairwise win-loss data from focal follow and ad-lib observations collected over the entire behavioral sampling period. Ranks were calculated using only data from male-male interactions. These win-loss data included the IDs of the winner and loser of the interaction. Individuals that gave contact aggression, noncontact aggression, or a threat, displaced another individual, or received a submission or fear grimace were recorded as winners. Individuals that received contact aggression, noncontact aggression, or a threat, were displaced, or gave submission or a fear grimace were recorded as losers. Win-loss matrices were constructed using these pairwise data. Briefly, we set winners as columns and losers as rows, and ordered the matrix such that the maximum number of cells containing interaction data fell above the diagonal, following the principle of transitivity (if A outranks B and B outranks C, A outranks C). We included all males followed for behavioral data collection in the hierarchies, regardless of whether they were sampled for morphometric data collection. Males that were observed for less than two standard deviations below the mean focal time were excluded from the hierarchies. The dominance matrix for group R contained a large number of reversals (interactions falling below the diagonal), particularly in mid-ranking males, likely due to rank instability throughout the year. We used proportional ranks (the percentage of within-group males that a focal male dominated) in our analyses to control for differences in group size. We also measured the correlation between our dominance ranks and group tenure length at the end of the sampling period, as rhesus macaque males tend to acquire rank through succession (Manson 1995; Berard 1999). If a male changed groups during the study period, only tenure in his last group during was included in the calculation. Where both data were available, dominance rank and tenure length were weakly, but significantly, correlated across the full dataset

(Pearson’s r = -0.242 p = 0.004), but not significantly correlated in the subset of males measured (Pearson’s r = -0.200, p = 0.117). This discrepancy may be due to the observed instability in the group R dominance hierarchy during the study period.

Morphometric Data

One trained observer collected morphometric data for an unrelated project during the 2015 annual capture-release season (October to December). This dataset contained 66 males from groups F, R, and V who were followed for behavioral data collection in 2016 and for which dominance rank data were available. All of these animals were captured and anaesthetized by trained CPRC staff and released back onto Cayo Santiago after data collection. We used two measurements in our analyses: body mass (collected using a hanging scale and converted from pounds to kilograms) and upper canine height (measured as the length of the canine from the gingival margin to the tip of the tooth, in millimeters (Plavcan 1990)). Upper canine height was measured on both the right and left canine teeth; we used the maximum value per animal in our analyses. We included all canine height and body mass data in our analyses, including data from worn and broken teeth (n = 4 males with noted broken teeth). Three males in the sample had body masses above 15kg, a threshold other studies have used to measure obesity in rhesus macaques (e.g., (Hamilton et al. 1972)). These three males were between 11.5 and 12.5 years old and therefore in their reproductive prime (Dubuc, Ruiz-Lambides, et al. 2014). We have kept them in our sample because we believe these higher body masses represent real biological variation in this population. Canine height and body mass were correlated (Pearson’s r = 0.282, p = 0.029).

Table 1. Summary statistics for morphometric data

Trait	**n**	**Mean**	**Range**	**CV (%)**
Canine height	66	18.56mm	8.03mm - 27.32mm	15.06%
Body mass	66	11.23kg	7.67kg -16.78kg	16.86%
Age	66	9.54 years	6.01 years – 20.71 years	33.26%

Data aggregation

We aligned morphometric data from the 2015 capture-release period (October to December) with behavioral and rank data from the following mating season and subsequent months (January to October 2016), since male body mass during the birth season best reflects their ability to engage in energetically costly strategies during the mating season (Bercovitch 1992; Bercovitch 1997; Higham et al. 2011). Rhesus macaque males build condition during the birth season (which coincides with the capture-release period), and then use those energy reserves to compete through endurance rivalry during the mating season; males who are in better condition at the end of the birth season tend to be in better condition during the subsequent mating season (Bercovitch 1992; Bercovitch 1997; Higham et al. 2011).

In total, the aggregated behavioral and morphometric dataset contained data on 482 male-male agonistic interactions (402 focal, 80 ad-lib) between the 66 males for which morphological and dominance rank data were available. Of these interactions, only eight were contact aggression. The rate of agonism among males with morphological and dominance rank data was 1.19 interactions/hour (402 focal interactions over 339 focal hours). The mean number of interactions per sampled male was 13 (range: 1 – 53) and the mean number of interactions per sampled dyad was 1.73 (range: 1 – 9). 186 of these interactions took place during the mating season. There were 2347 male-male agonistic interactions (1900 focal and 447 ad-lib) in the entire behavioral dataset, 61 of which were contact aggression. 1066 of these interactions took place during the mating season. The average rate of agonism in the entire dataset was 2.49 interactions/hour (1881 focal interactions over 755.5 focal hours). The mean number of interactions per male in the entire behavioral dataset was 30.36 (range: 4 – 82) and the mean number of interactions per dyad was 1.70 (range 1 – 14). There was instability in male group membership and in the male dominance hierarchy in group R in 2016, which may explain the high rate of agonism in the entire dataset. Nonetheless, the data analyzed here represent a subset of males and male-male interactions across the three groups (n = 19 group F males, n = 31 group R males, n = 19 group V males).

Data statement

All data and code will be made available on a public repository upon publication. During peer review, data and code to reproduce the analyses in this manuscript are available via this Dropbox link: https://www.dropbox.com/sh/2miph4sneo1oxtg/AAANYWO7fnBpiRm643yqhrIqa?dl=0.

Statistical analyses

We ran all statistical analyses in R version 4.0.3 (R Development Core Team 2020). We ran all generalized linear mixed models in the glmmTMB package, version 1.2.0.1 (Brooks et al. 2017), and assessed residual diagnostics using the DHARMa package, version 0.3.3.0 (Hartig 2020). We used DHARMa functions to check the following diagnostics: normality of residuals, overdispersion of residuals, outliers in the residuals, and correlations between residuals and fitted values. These tests revealed only one violation of assumptions for only one model presented in the main text. We provide additional details below regarding this model, and models not presented that violated some of these assumptions.

Morphometrics and dominance rank

We tested whether **(1) morphometrics and dominance rank** were related using generalized linear models (GLMMs) with a beta error structure. First, we transformed proportional ranks so that they fit a beta distribution by assigning animals with a proportional rank of 1 to 0.99 and animals with a proportional rank of 0 to 0.01. We set dominance rank as the response variable, canine height, body mass, age, and social group as fixed effects, and focal ID as a random effect to account for repeated measures on the same male. This analysis included 69 data points on 66 males. There are some repeated measures because three males dispersed during the course of the study period and therefore appear in data from more than one social group.

Occurrence of agonistic interactions

We tested whether **(2)** body mass, canine height, or dominance rank influenced the **occurrence of agonistic interactions** between male-male dyads using GLMMs with a binomial (Bernoulli) error structure with a “cloglog” link function. Analyses had one data point per potentially interacting male-male dyad per focal-day (n = 41,728 potential interactions, n = 805 male-male dyads). Males were very rarely in very close proximity. We assumed that because rhesus macaque groups are relatively stable on a day-to-day basis and group members travel together, all males should have an equal opportunity to interact with all other males in the group. For the purposes of our analyses, we considered two males to be potentially interacting if they were both present in the group on a particular day. We estimated daily presence based on CPRC monthly census files, under the assumption stated above that groups are generally stable, such that monthly presence is a good approximation for daily presence. We set whether or not the dyad interacted agonistically as the response variable, the absolute value of the difference in canine height, body mass, and dominance rank per dyad, plus social group as fixed effects, dyad ID and season (mating/birth) as random effects, and observation time per focal male per dyad (log) as an offset. DHARMa diagnostic tests on residuals from this model detected some outlying values. We did not alter the data or model structure as the outlier test is conservative, and we believe outlying values represent real variation and should not be removed from analyses.

Outcome of contact aggression

As described above, of the 482 agonistic interactions in our dataset, only eight were contact aggression, precluding our ability to run models on these data to test whether body mass, canine height, or dominance rank influenced the outcome of **contact aggression** between male-male dyads **(3.1)**. We describe these interactions qualitatively below.

Outcome of all agonistic interactions

We used two approaches to investigate how **(3.2)** body mass, canine height, and dominance rank predicted the **outcome of agonistic interactions** between males. We used binomial (Bernoulli) GLMMs with a logit link function to investigate whether differences in body mass, canine height, or rank influenced the likelihood of aggression or submission occurring between a male-male dyad. We set the type of agonistic interaction (aggression (1)/submission (0)) as the response variable, the difference between males in body mass, canine size, and rank (winner value minus loser value), plus social group as fixed effects, and dyad ID as a random effect. Both ad-lib and focal data were included in this analysis (n = 478 interactions, n = 277 dyads), but only agonistic interactions that could clearly be categorized as aggressive or submissive were included in this model (submit/threat was excluded). We also used binomial (Bernoulli) GLMMs with a logit link function to test whether body mass, canine height, or rank predicted whether a focal male won an agonistic interaction. We set whether or not the focal male won (0/1) as the response variable, canine height, body mass, dominance rank, and social group as fixed effects, and focal ID as a random effect. Focal ID was used as a random effect because the model did not converge with dyad ID set as a random effect. This model only used focal data to facilitate controlling for the direction of the interaction (n = 402 interactions, n = 65 focal males; one male measured for morphometric data and dominance rank was never a focal male in a male-male agonistic interaction). Dominance rank was used in this model purely to control for its potential effects. We attempted to run a version of this model without dominance rank, but there was heteroscedasticity in the residuals, so we do not present results from that model here.

Ethical note

This research was conducted following Animal Behavior Society guidelines for the ethical treatment of animals. All data were conducted following protocols approved by the University of Puerto Rico Institutional Animal Care and Use Committee (protocol numbers: A150116 and A6850108).

Results

1) Morphometrics and dominance rank

Neither canine height (z-value = -0.485, p = 0.627) nor body mass (z-value = 0.415, p = 0.627) predicted dominance rank after controlling for age and social group (Table 2). Although older males tended to be higher-ranking, this relationship was not statistically significant (z-value = 1.623, p = 0.105) (Table 2).

Table 2. Results from beta models testing relationships between morphometrics and dominance rank (n = 69 unique male-group combinations).

Term	**Estimate**	**Standard Error**	**z-value**	**p-value**
Intercept	-0.617	1.075	-0.574	0.566
Canine height	-0.021	0.043	-0.485	0.627
Body mass	0.032	0.079	0.415	0.678
Age	0.068	0.042	1.623	0.105
Group (Group F)[1]	-0.477	0.324	-1.474	0.140
Group (Group V)[1]	-0.174	0.318	-0.547	0.584

[1] Group had three levels: F, R, and V. Groups F and V were compared to Group R.

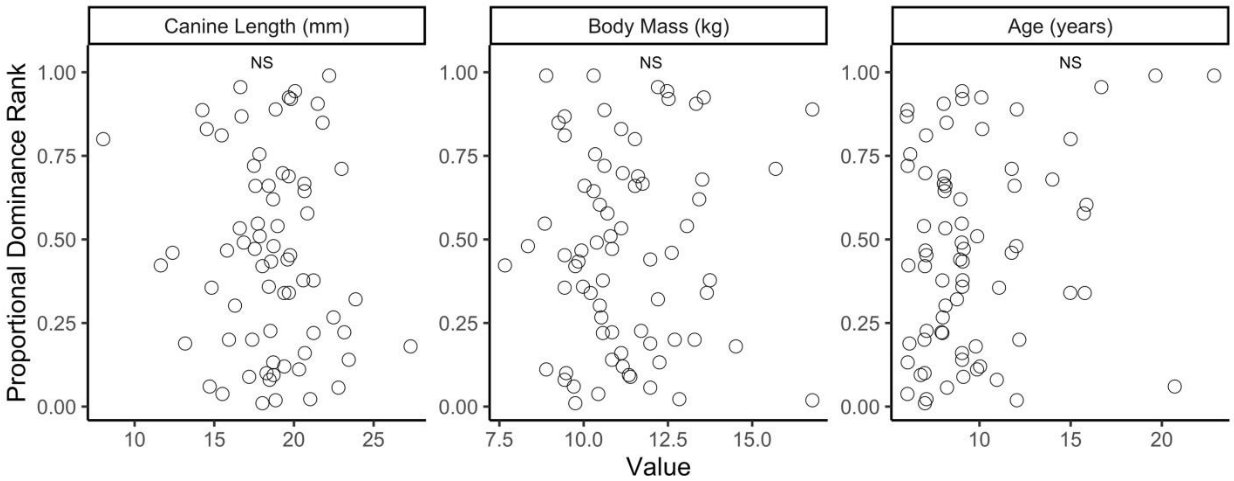

Figure 1. Raw data plots of canine height, body mass, and age by dominance rank (n = 69 males). NS = non-significant predictor ($p \geq 0.05$).

2) Occurrence of agonistic interactions

Differences in dominance rank (z-value = -2.84, p = 0.004), but not in canine height (z-value = -1.53, p = 0.125) or body mass (z-value = 0.71, p = 0.476), predicted the likelihood of agonism between male-male dyads, after controlling for social group (Table 5). Males who were more similar in dominance rank were more likely to interact agonistically than males with large differences in dominance rank. There were also differences in slope estimates between groups R and group V (z-value = -2.67, p = 0.008) (Table 3). The likelihood of agonism was higher in group R than in group V, but not different between groups R and F.

Table 3. Results from binomial models testing relationships between morphometrics and the likelihood of agonism between male-male dyads. Statistically significant results ($p < 0.05$) are bolded.

Term	**Estimate**	**Standard Error**	**z-value**	**p-value**	**Odds Ratio**
Intercept	-6.988	0.174	-40.03	**< 2e-16**	
Difference in dominance rank	-0.824	0.290	-2.84	**0.004**	0.439
Difference in canine height	-0.039	0.025	-1.53	0.125	0.962
Difference in body mass	0.032	0.044	0.71	0.476	1.032
Group (Group F)[1]	-0.225	0.166	-1.34	0.181	0.801
Group (Group V)[1]	-0.479	0.179	-2.67	**0.008**	0.619

[1] Group had three levels: F, R, and V. Groups F and V were compared to Group R.

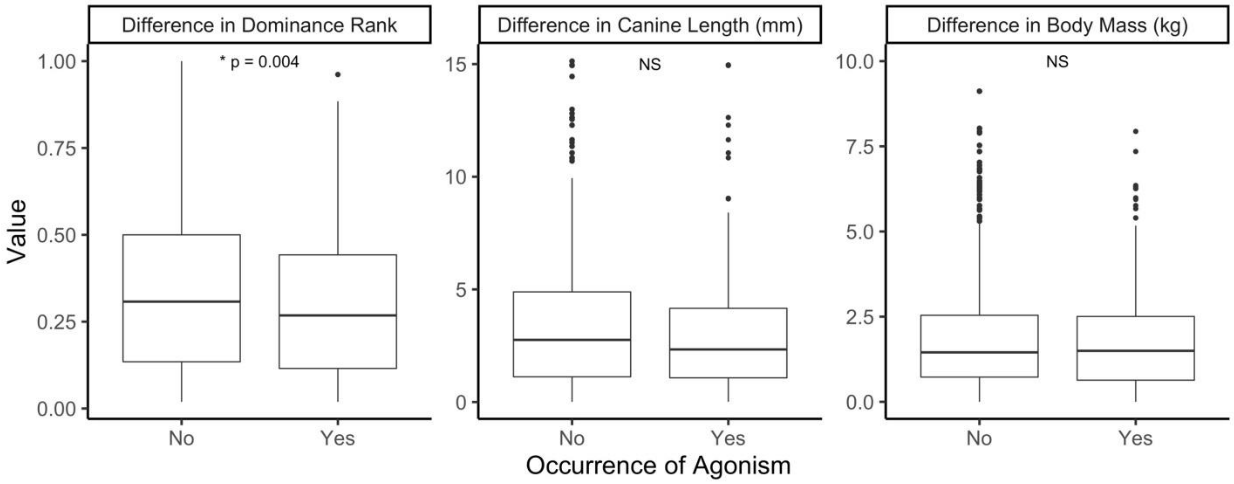

Figure 2. Raw data plots of the absolute value of differences in dominance rank, canine height, and body mass by the occurrence of agonistic interactions between dyads (n = 41,728 potentially occurring interactions between 805 unique dyads). P-values are taken from model output. NS = non-significant predictor ($p \geq 0.05$).

3.1) Outcome of contact aggression

Of the eight instances of contact aggression, the winner was higher-ranking in seven cases. Where the winner was not higher-ranking, the winner also had lower body mass, but had very slightly larger canines (the winner's canine height was 0.01mm longer than the loser's canine height). This difference could encompass measurement error. The winner had larger canines in six out of eight cases, and higher body mass in five out of eight cases.

3.2) Outcome of all agonistic interactions

Differences in dominance rank (z-value = -2.164, p = 0.030), but not in canine height (z-value = 0.422, p = 0.673) or body mass (z-value = 0.123, p = 0.902), influenced the likelihood of aggression occurring over submission between male-male dyads, while controlling for social group (Table 4). Interactions between males closer in dominance rank were more often characterized by aggression than submission when compared to interactions where the winner was higher ranking than the loser (Figure 3).

Table 4. Results from binomial models testing relationships between morphometrics and the likelihood of aggression or submission between male-male dyads. Statistically significant results ($p < 0.05$) are bolded.

Term	Estimate	Standard Error	z-value	p-value	Odds Ratio
Intercept	-0.499	0.146	-3.414	**0.001**	
Difference in dominance rank	-0.774	0.357	-2.164	**0.030**	0.461
Difference in canine height	0.011	0.026	0.422	0.673	1.011
Difference in body mass	0.005	0.046	0.123	0.902	1.006
Group (Group F)[1]	-0.297	0.254	-1.168	0.242	0.743
Group (Group V)[1]	-0.412	0.280	-1.471	0.141	0.662

[1] Group had three levels: F, R, and V. Groups F and V were compared to Group R.

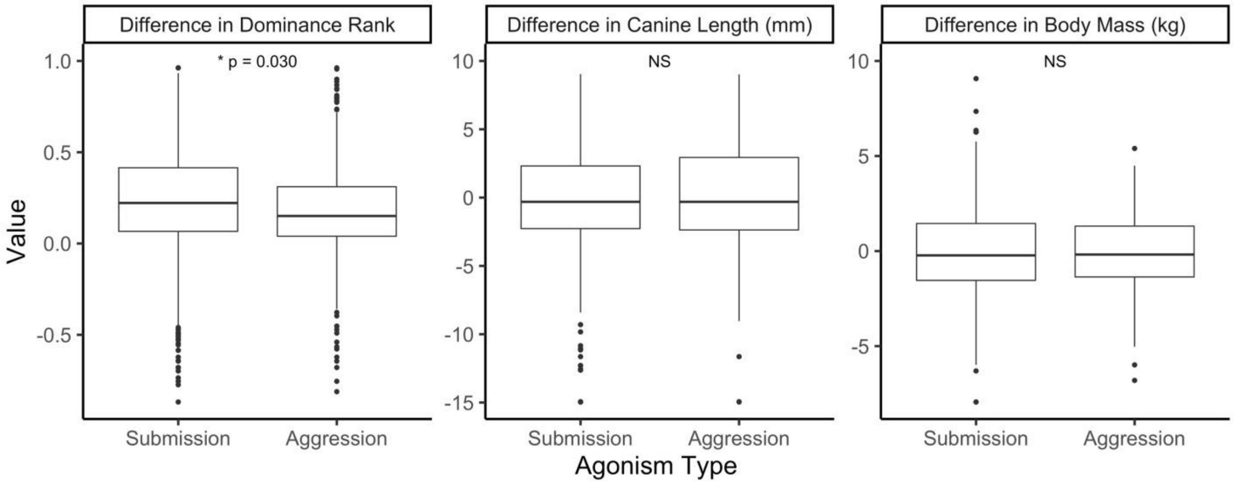

Figure 3. Raw data plots of differences in dominance rank, canine height, and body mass (winner value minus loser value) by the occurrence of aggression or submission between dyads (n = 478 interactions, 277 unique dyads). P-values are taken from model output. NS = non-significant predictor ($p \geq 0.05$).

Dominance rank (z-value = 6.260, p = 3.86e-10), but not canine height (z-value = -0.895, p = 0.371) nor body mass (z-value = 1.440, p = 0.150) predicted the likelihood of the focal male winning an agonistic interaction (Table 5). Higher-ranking males were more likely to win an agonistic interaction.

Table 5. Results from binomial models testing relationships between morphometrics and the likelihood of a focal male winning an agonistic interaction. Statistically significant results ($p < 0.05$) are bolded.

Term	**Estimate**	**Standard Error**	**z-value**	**p-value**	**Odds Ratio**
Intercept	-3.372	1.460	-2.310	**0.021**	
Focal dominance rank	4.191	0.670	6.260	**3.86e-10**	66.094
Focal canine height	-0.054	0.061	-0.895	0.371	0.947
Focal body mass	0.151	0.105	1.440	0.150	1.162
Group (Group F)[1]	0.372	0.435	0.855	0.393	1.450
Group (Group V)[1]	0.394	0.442	0.892	0.372	1.483

[1] Group had three levels: F, R, and V. Groups F and V were compared to Group R.

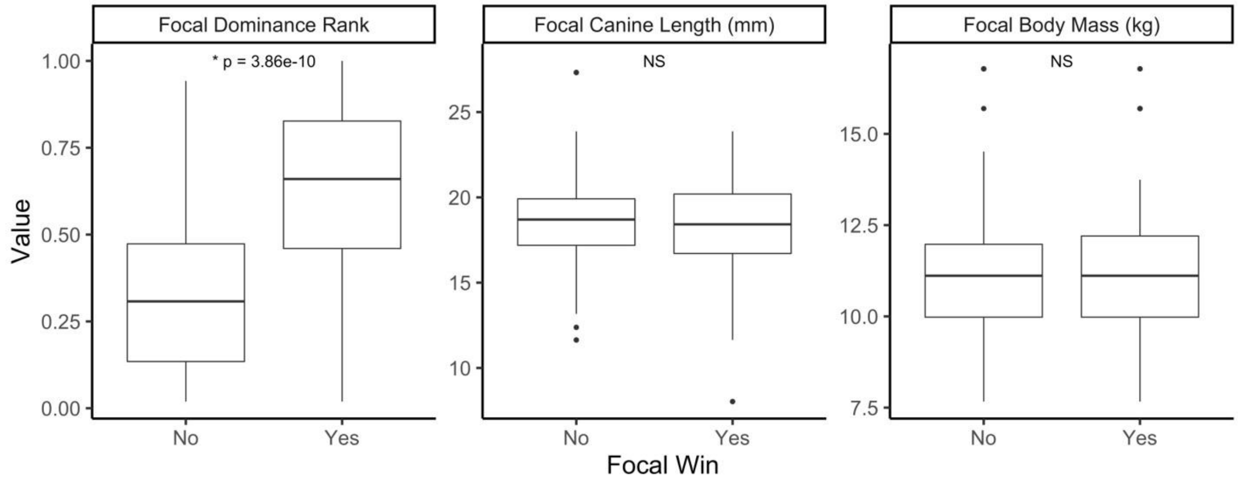

Figure 4. Raw data plots of dominance rank, canine height, and body mass by whether or not a focal male won an agonistic interaction (n = 402 interactions, 65 unique focal males). P-values are taken from model output. NS = non-significant predictor ($p \geq 0.05$).

Discussion

Our results suggest that body mass and canine height do not play a role in the acquisition of dominance rank, nor do they function as signals or weapons in male-male agonistic interactions, and that therefore, these traits do not confer a strong competitive advantage in male rhesus macaques in the study population. We found that **(P1b)** neither body mass nor canine size was correlated with dominance rank, that neither morphometric variable predicted the **(P2b)** occurrence or **(P3.2b)** outcome of dyadic agonistic interactions between male rhesus macaques after controlling for social group. Agonistic interactions were rarely settled using contact aggression. Anecdotally, males that were higher-ranking and larger in body mass and canine height were more likely to win interactions involving contact aggression. Dominance rank influenced the occurrence and outcome of agonistic behavior independently of canine height or body mass. Males more similar in dominance rank were more likely to interact agonistically than males very different in dominance rank, and when these interactions occurred, they were more often characterized by aggression than submission.

We found that neither canine height nor body mass correlated with dominance rank. If weaponry helped males acquire high rank, we would expect to see a correlation between canine height and/or body mass and dominance rank. Our findings are consistent with predictions about the function of weaponry in groups with reduced levels of male-male competition where males cannot monopolize access to females (van Noordwijk and van Schaik 2004). Much of the available evidence demonstrates that, in species where male reproductive skew based on dominance rank is high, males contest dominance rank, and body size and weaponry tend to correlate with dominance rank (e.g., crest height and back breadth in mountain gorillas (Wright et al. 2019), canine height in baboons *Papio cynocephalus* (among high-ranking males only) (Galbany et al. 2015), body mass in fallow deer (McElligott et al. 2001), and body size in northern elephant seals (Haley et al. 1994)). Rhesus macaque males, however experience low levels of direct male-male competition and do not usually contest dominance rank ((Manson 1995; Higham and Maestripieri 2014), but see Higham and Maestripieri (2010) and Georgiev (2016) for exceptions). As expected given their low degree of reproductive skew based on dominance rank, they queue for dominance; males enter new groups at the bottom of the hierarchy and their rank increases with group tenure length, as higher-ranking males either secondarily disperse or die (Manson 1995; Higham and Maestripieri 2014). In systems where males queue for dominance, fighting ability is not necessarily correlated with rank, and weaponry is predicted to be under weaker selection (van Noordwijk and van Schaik 2004; Higham and Maestripieri 2014). Our findings that body mass and canine height do not correlate with dominance rank are consistent with this prediction.

We also found that agonistic interactions involving contact aggression were rare, and that neither canine height nor body mass predicted the occurrence or outcome of agonistic interactions among males. The rarity of contact aggression suggests that male-male agonistic interactions are usually not settled by physical fighting, creating less potential for weaponry to influence contest outcomes. However, anecdotally, winners of contact aggression interactions tended to be larger than losers. In species where males compete directly for mating opportunities, body size and weaponry often plays a role in settling contests (e.g., mountain gorillas (Wright et al. 2019), caribou (Barrette and Vandal 1990)). However, male weaponry does not always influence fighting behavior after controlling for rank (e.g., fallow deer Jennings et al. (2006)), highlighting the fact that the outcome of male-male contests is not always determined by size differences alone. Our findings suggest that body size and weaponry are not important in determining the likelihood or outcome of agonism in male rhesus macaques. Instead, dominance rank mitigates the occurrence of agonistic interactions between males independently of body size and weaponry. Our dominance rank results, but not our results from body mass or canine height, are consistent with game theoretic models of animal behavior (Smith 1979), which predict that animals closely-matched in competitive ability are more likely to fight, while animals with large asymmetries in competitive ability will avoid fights (see data from savannah baboons *Papio ursinus* (Kitchen et al. 2003) and mountain gorillas (Wright et al. 2019)).

Our findings are also consistent with previous work on sexual selection in rhesus macaque males from Cayo Santiago. Rhesus macaque males primarily compete through indirect mechanisms such as sperm competition (Harcourt et al. 1981; Bercovitch and Rodriguez 1993) and endurance rivalry (Bercovitch 1992; Bercovitch 1997; Higham et al. 2011; Higham and Maestripieri 2014), rather than direct male-male competition. Rhesus macaque males are also able to obtain mating opportunities using different strategies; high-ranking males often undertake consortships (with varying levels of success (Dubuc et al. 2011; Dubuc et al. 2012)), while low-ranking males mate using sneak copulations (Higham and Maestripieri 2014). Furthermore, females are able to exercise some degree of direct mate choice (e.g., based on facial coloration Dubuc et al. (2014)). Interestingly, although neither body mass nor canine size function as signals in male-male agonistic interactions, rhesus macaque male facial coloration does (Petersdorf et al. 2017). Taken together, these results demonstrate that rhesus macaque males have undergone selection on a signal that influences male-male competition; but the signal is color rather than weaponry. These lines of evidence suggest that there is limited scope for large body size and weaponry to influence male reproductive success, at least in this population. Given the current competitive regime of rhesus macaque males, it is possible that the observed sexual dimorphism in body mass and canine height are evolutionarily lagged traits, which may have influenced male-male contests in the potentially more dimorphic ancestor of rhesus macaques, but which no longer have such a function.

One important caveat to consider in relation to our results is that environmental conditions on Cayo Santiago differ from conditions in the wild. The rhesus macaques on Cayo Santiago are provisioned and group sizes are larger on average than in the wild. Group sizes on Cayo Santiago range from 50 to 500 animals, while in the wild, groups typically comprise 20 to 250 individuals (Southwick and Siddiqi 2011). It is possible that the effects of provisioning combined with a lack of predation, and in turn, these large group sizes, have influenced our results, given that group size is one of the key factors in determining female fertile phase synchrony, and, by extension, the nature of male competitive regimes (Emlen and Oring 1977; McClintock 1983). Indeed, while rare, there have been some reports of alpha-male takeovers in rhesus macaques (Vandenbergh 1967; Neville 1968; Georgiev et al. 2016). That prediction that group size may affect dominance acquisition pattern is supported by reports of alpha-male takeovers and contests over dominance rank in smaller groups of Japanese macaques, a species often, like rhesus, characterized by large group sizes and males queueing for dominance rank (Sprague 1992; Sprague 1996; Yamagiwa and Hill 1998; Hayakawa and Soltis 2011). However, large group size and provisioning alone do not appear sufficient to explain reports of dominance acquisition through succession in species like rhesus macaques and Japanese macaques. Indeed, to our knowledge, such behavior has never been reported for other populations of Papionin species even when these populations are provisioned and group size is large (e.g., captive mandrills at Centre International de Recherches Médicales de Franceville, Gabon (Setchell and Dixson 2001), hamadryas baboons at the German Primate Center (Zinner and Deschner 2000)). This suggests that queuing for dominance is part of the behavioral repertoire of some species but not others. Furthermore, the idea that rhesus macaques experience lower direct and high indirect male-male competition than some other Papinions is supported by morphological evidence: males are characterized by relatively low canine and body size dimorphism and large relative testis volume of this species compared to other Papionins (Harcourt et al. 1981; Plavcan 2004). Recent studies of Kinda baboons, another species with relatively small body and canine size dimorphism and large relative testis volume have also found that males of this species queue for dominance (Petersdorf et al. 2019). However, additional studies of the function of male weaponry in wild populations of rhesus macaques are necessary to confirm whether our findings apply to all populations of the species.

A number of outstanding questions remain. Additional work is needed to investigate if body mass and canine height influence the outcome of agonistic encounters involving contact aggression, given that agonistic interactions involving contact aggression are rare. Furthermore, intersexual selection may have influenced the evolution of male body mass and canine height in rhesus macaques. Female rhesus macaques may prefer males with higher body masses (or larger body size), or larger canines (e.g., Berglund et al (1996)). It would be possible to test whether females prefer males with larger body sizes by collecting photogrammetric data on male body size in the field and determining whether females preferentially mate with larger-bodied males. Furthermore, in order for male body size and weaponry to be sexually selected, they should influence reproductive success. To date, although neither body mass nor canine height correlate with average annual fecundity (Kimock et al. 2019), whether these traits influence lifetime reproductive success in rhesus macaques is unknown. More studies on female choice for male weaponry, and on how male weaponry influences reproductive success across a range of timescales, are needed to elucidate why and how male body mass and canine height have evolved in rhesus macaques.

Our results add to growing evidence that weaponry and large body size do not always function as weapons or signals in agonistic interactions between males. They also highlight the need for detailed studies of trait function in order to determine whether male armaments act as signals, weapons, or both, in male-male competition, and which factors best predict the occurrence and outcome of male-male contests.

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Ethical note

This research was conducted following Animal Behavior Society guidelines for the ethical treatment of animals. All data were conducted following protocols approved by the University of Puerto Rico Institutional Animal Care and Use Committee (protocol numbers: A150116 and A6850108).