



Male body size, dominance rank and strategic use of aggression in a group-living mammal

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Body size is a key determinant of male fighting ability and reproductive success in many animal species, but relationships between these variables have only rarely been examined in group-living animals in which body size often correlates with dominance rank. We examined the relationships between body size (crest height, back breadth and body length), dominance rank, alpha male tenure length, number of adult females and patterns of aggression in 26 wild adult male mountain gorillas, *Gorilla beringei beringei*, living in multimale groups. A composite measure combining crest height and back breadth (variables were highly correlated and combined into a crest–back score), but not body length, significantly correlated with dominance rank, alpha male tenure length and number of adult females per group. The alpha male had the largest crest–back score in six of the seven groups, and in the majority of dyads the male with the higher crest–back score was higher ranking. The frequency (and intensity on mating days) of aggressive contests was higher between males close in rank. Additionally, aggression occurred more frequently when the initiator was larger than the recipient. Our results suggest that factors other than body size are likely to influence dominance rank, but large size helps males attain and retain high dominance rank, probably leading to greater reproductive success. Further studies on how the timing and intensity of male–male competition influences life history trade-offs between investment in secondary sexual characteristics, body condition and survival may explain variance in lifetime reproductive success within and between species.

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According to sexual selection theory, traits that help males win fights such as large body size or weapons are expected to be under strong selection, resulting in large males having high reproductive success (Andersson, 1994; Darwin, 1871). Selection for large male size can also be the result of female mate choice or sexual coercion (Kuijper, Pen, & Weissing, 2012; Smuts & Smuts, 1993). In group-living species, dominance rank, which typically reflects individual fighting ability, is often strongly correlated with body size and/or weaponry (Clutton-Brock, 2017; Galbany, Tung, Altmann, & Alberts, 2015; McElligott et al., 2001; Pelletier & Festa-Bianchet, 2006; but see: Feh, 1990; Kitchen, Seyfarth, Fischer, & Cheney, 2003; Lawler, Richard, & Riley, 2005; Lidgard, Boness, Bowen, & McMillan, 2005; Neumann, Assahad, Hammerschmidt, Perwitasari-Farajallah, &

Engelhardt, 2010; Pusey, Oehlert, Williams, & Goodall, 2005; Spong, Hodge, Young, & Clutton-Brock, 2008). However, fighting ability and dominance rank may be influenced by traits other than body size, including physical condition, experience, age, personality, skill and/or coalitionary support (Arnott & Elwood, 2009; Briffa & Sneddon, 2006; Holekamp & Smale, 1991; Schülke, Bhagavatula, Vigilant, & Ostner, 2010). Moreover, because of the difficulties of measuring body size in wild animals, remarkably few studies have examined the relationship between body size, dominance rank and reproductive success in group-living animals (Bergeron, Grignolio, Apollonio, Shipley, & Festa-Bianchet, 2010; Plavcan, 2004; Spong et al., 2008).

Dominance rank is typically attained via competitive interactions with the outcome primarily reflecting asymmetries in fighting ability or resource-holding potential (RHP) between contestants (Clutton-Brock & Huchard, 2013; Parker, 1974). Because aggression is costly, males are expected to be under strong selection to assess the costs and benefits associated with initiating,

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escalating and retreating in contests (Enquist & Leimar, 1983; Thompson & Georgiev, 2014). High-ranking males tend to be more aggressive than low-ranking ones (e.g. Muller & Wrangham, 2004). However, high-ranking individuals may not need to use frequent aggression to monopolize access to resources, as lower ranking individuals often avoid contests with them (Sapolsky, 2005).

According to evolutionary game theory, evenly matched contestants are expected to exhibit a higher frequency and intensity of aggression than those with larger asymmetries in RHP (Enquist & Leimar, 1983; Parker, 1974). Because the outcome of such contests is less clear, there may be a greater need to 'clarify' dominance relationships and/or there is a higher likelihood that the slightly weaker individual may be able to win (Arnott & Elwood, 2009; Bergeron et al., 2010; Jennings, Gammell, Carlin, & Hayden, 2006). However, factors other than asymmetries in fighting ability may play a role in aggressive contests. Within stable social groups, the decision to initiate, escalate and retreat in contests between familiar males is thought also to be based on the outcome of earlier encounters reflecting previously established dominance relationships (Archer, 1988). The frequency and intensity of aggression are often greater during reproductive periods than nonreproductive periods, which probably reflects competition for a high-value resource (e.g. Muller & Wrangham, 2004). Moreover, patterns of aggression involving physical contact and fighting may better reflect asymmetries in RHP than lower intensity noncontact aggression (such as vocal and visual displays), which mainly serve to signal the intention to fight and can therefore be more easily faked (Arnott & Elwood, 2009; Setchell & Wickings, 2005). In summary, selection is thought to favour males that minimize the frequency and severity of aggressive interactions, but simultaneously favour the strategic use of aggression to attain and retain high dominance rank and access to females (Arnott & Elwood, 2009; Clutton-Brock & Huchard, 2013).

Gorillas are characterized by female defence polygyny and are one of the most sexually (size) dimorphic mammal species, indicating that male–male competition is important for attaining alpha status and high reproductive success (Harcourt & Stewart, 2007; Plavcan, 2001). In western lowland gorillas, *Gorilla gorilla gorilla*, male body size (body length, crest size and gluteal muscle size) is correlated positively with the number of adult females in the group (Breuer, Robbins, Boesch, & Robbins, 2012; Caillaud, Levréro, Gatti, Ménard, & Raymond, 2008). Because lowland gorillas live almost exclusively in one-male groups (Robbins & Robbins, 2018), which is assumed to be the ancestral state for gorillas (Harcourt & Stewart, 2007), these studies were not able to examine within-group male–male competition. By contrast, multimale groups are common in mountain gorillas (Robbins & Robbins, 2018) which is puzzling given that gorillas lack the typical physical characteristics of species living in multimale group structures, such as large testes in males and pronounced female sexual swellings (Harcourt & Stewart, 2007). However, patterns of within-group male–male competition in mountain gorillas appear to follow established predictions for multimale groups (Ostner & Schülke, 2014; Plavcan, 2004), such as strong male–male competition resulting in dominance hierarchies and increased levels of aggression on days when females are in oestrus (Robbins, 1996, 2003; Sicotte, 1994). Nevertheless, mountain gorilla males only rarely fight using high-intensity contact aggression, although signs of injury are not uncommon and aggression can be fatal (Robbins, 1996; Rosenbaum, Vecellio, & Stoinski, 2016).

The assumption that body size correlates positively with dominance rank and how both these variables relate to patterns of male–male aggression in multimale mountain gorilla groups have not been studied. Alpha male status (highest ranking male in a

group), alpha male tenure length (the duration a male is the alpha male in a group) and number of adult females in the group are the main sources of variation in the reproductive success of male mountain gorillas (Robbins et al., 2014), and alpha males sire between 72 and 85% of infants in multimale groups (Bradley et al., 2005; Vigilant et al., 2015). However, it is unknown whether differences in alpha male body size drive variation in these components. Examining these relationships in multimale groups of a species that forms both one-male and multimale groups may help our understanding of the evolution of variable mating systems and life history patterns in social animals (Plavcan, 2004).

To examine the relationships between body size, dominance rank, correlates of reproductive success and patterns of aggression, we measured three morphological traits associated with body size (crest height, back breadth and body length) using the noninvasive parallel laser method (Bergeron, 2007; Galbany et al., 2016; Rothman et al., 2008) and collected behavioural and demographic data from nine mountain gorilla groups. As we expected body size to be a key determinant of fighting ability, we first tested whether body size correlated positively with dominance rank. Second, we tested whether body size and alpha rank correlated positively with two correlates of reproductive success: alpha male tenure length and number of females in the group. Third, we examined the use of intragroup aggression in relation to body size and dominance rank. We predicted that body size and dominance rank correlate positively with (1) frequency of aggression and (2) the probability of using higher intensity contact aggression. We also predicted that similar matched dyads in dominance rank and body size (with low asymmetries) would exhibit a higher frequency and intensity of aggression than more unevenly matched dyads. Lastly, we predicted a higher frequency and intensity of aggression on mating days than nonmating days.

METHODS

Study Population

The study was conducted on 26 adult male silverbacks (males older than 12 years, Robbins, 2011) from nine social groups (seven multimale and two one-male) monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center, Volcanoes National Park, Rwanda. The average number of males in the seven multimale groups was three (range 2–6). Unless indicated otherwise, the study period spanned 2.5 years between January 2014 and July 2016.

Behavioural Data Collection

Observations were collected by multiple observers over 2116 group-days and lasted for approximately 4 h/day, according to regulations set by the Rwanda Development Board to minimize disturbance to the gorillas. We recorded displacements and avoidances (approach and retreat interactions) and aggressive interactions among the 24 males residing in the seven multimale groups during focal animal sampling periods and ad libitum data collection (Altmann, 1974). Analyses of rates of aggression exclusively used data from focal animal sampling, which was mainly done in 50 min periods (91%; range 20–50 min; similar to the long-term data collection protocol used by the Dian Fossey Gorilla Fund's Karisoke Research Center). The mean number of hours of focal animal sampling per male was 133 h (range 28–307 h; total: 2927 h).

Aggressive interactions were divided into contact and noncontact aggression. Noncontact aggressive interactions included cough grunting, screaming and aggressive displays such as chest beating or smashing vegetation (Robbins, 1996). Contact aggression

included biting, hitting, kicking, dragging and shoving (Robbins, 1996). The identities of the aggressor and the recipient were recorded and a categorical variable was included in the analyses to indicate whether a mating had been observed between adult individuals in the group on the day of observation (henceforth mating day) or not (nonmating day, Robbins, 2003). Matings were observed on 404 group-days (19%).

Photogrammetry

We used the noninvasive parallel laser method to measure three traits associated with body size: crest height, body length and back breadth (Bergeron, 2007; Rothman et al., 2008; Galbany et al., 2016, 2017). This method relies on two parallel lasers projected onto the target object plane separated by a known distance, which is then used as a scale to measure morphological traits of interest. The high accuracy and precision of the parallel laser method has been validated in captive lowland gorillas and wild mountain gorillas (Galbany et al., 2016, 2017). Photos were collected and measured by E.W. and J.G. We used the same equipment (including a similar laser device), measurement protocols and landmarks as Galbany et al. (2016, 2017). Measurements were obtained from an average of nine photos per male and trait (range 3–24) totalling 694 photos of 26 males. We used the average measurement of each trait per male in the analyses. Seasonal changes in body size are not expected in mountain gorillas owing to low variability in food availability in their habitat (Watts, 1984; Wright et al., 2015). Photos were measured in ImageJ (Abramoff, Magalhães, & Ram, 2004); see Appendix Tables A1 and A2 for details of photogrammetry error and validation.

Body Size Variables

Since the measurements of the three morphological traits (crest height, body length and back breadth) could be highly correlated, we ran a principal component analysis (PCA) based on the correlation matrix using the R function 'pccomp', to reduce redundancy and collinearity issues (see Appendix for details of the PCA). An initial PCA revealed that body length did not correlate strongly with either of the other two traits, nor did it load strongly on the one factor with eigenvalues ≥ 1 . Therefore, we ran a second PCA comprising only crest height and back breadth. The latter revealed one factor with an eigenvalue ≥ 1 , which explained 87% of the total variance. The two body size variables (back breadth and crest height) loaded strongly on the one factor (both loading factors = 0.71). Both the factor (hereafter named crest–back score) and body length were included in the analyses. Crest–back score and body length were weakly correlated ($r_s = 0.38$).

Dominance Hierarchies

Male dominance hierarchies in the multimale groups were based on displacements and avoidances (Harcourt & Stewart, 1989; Robbins, 1996) using interactions dating as far back as the formation of each group (2007–2013) or to 2000 for the PAB group which formed in 1993. We included all adult males present during this period (regardless of whether we had body size measurements). We employed the Elo-rating method (Albers & de Vries, 2001; Neumann et al., 2011) to calculate dominance hierarchies using the R package EloRating, version 0.43 (Neumann & Kulik, 2014). In contrast to matrix-based methods, Elo-rating continuously updates an individual's rank (Elo-score) after each interaction (Albers & de Vries, 2001; Neumann et al., 2011). The Elo-rating of the winner increases, while that of the loser decreases, with the amount of change being dependent on the probability of the individual with

the higher rating winning the interaction. Males were given a starting value of 1000 and k was set to 100. We applied the additional argument 'initt' which was set to 'bottom'. This argument assigns males entering the dominance hierarchy for the first time (maturing males) to the lowest rating on that day instead of the average starting Elo-rating value (see Foerster et al., 2016 for a similar approach) because young maturing males are known to be subordinate to all other adult males in the group (Harcourt & Stewart, 2007). We extracted Elo-ratings using the function 'extract.elo'. Ranks were standardized per group and day such that the highest rating male on a given day was assigned 1, the lowest was assigned 0 and ratings in between were set proportionally to their Elo-rating. The mean number of dominance interactions per male was 58 (20–157; SD = 35), excluding four males for which we had fewer than 10 interactions as they matured and entered the hierarchy analysis during the study period. Elo-rating revealed stable dominance hierarchies, with only one alpha male rank reversal during the study period (Appendix Fig. A1).

Statistical Analyses

Body size and dominance rank

We first tested the hypothesis that dominance rank correlates positively with crest–back score and body length in the multimale groups. We fitted a beta model implemented with the function 'glmmTMB' of the glmmTMB package (Brooks et al., 2017) with dominance rank (averaged over the study period) as the response variable, crest–back score and body length as predictor variables and group ID as a random effect. Each male was a data point ($N = 24$). Because our hypotheses concerning the effects of crest–back score and body length on dominance rank were based on the relative difference between males within a group rather than absolute values across groups we centred crest–back score and body length among males within each group to a mean of zero (similar to within-subject centering, van de Pol & Wright, 2009).

Body size, alpha male tenure length and number of adult females

Next, we tested the hypothesis that alpha male body size correlates positively with alpha male tenure length and the number of females in each group. We calculated the duration of 10 complete alpha male tenures (where both the start and end dates were known) and the average number of adult females during these tenures (females aged 8 and above, Robbins, 2011) in eight social groups between 1995 and 2017 (two one-male and six multimale groups). We fitted linear models (LMs) with Gaussian distribution and identity link to test the relationship between alpha body size (crest–back score and body length; predictors) and alpha male tenure length as well as the number of adult females (responses), which were log-transformed.

We then fitted four generalized linear mixed models (GLMMs) implemented with the function 'glmer.nb' and 'glmer' of the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2015) to examine the influence of both body size (crest–back score and body length) and dominance rank on patterns of aggression in multimale groups (see Appendix Statistical analysis: additional information and Table A3). The first two models focused on the influence of individual male properties, whereas the last two models examined dyadic properties (relative differences between dyads). As above, we centred crest–back score, body length and dominance rank among the unique combination of males present in each group at the time (group composition) to a mean of zero (similar to within-subject centering, van de Pol & Wright, 2009). All statistical analyses were conducted in R (R Core Team, 2017).

Frequency of aggression per male

The first GLMM with negative binomial error structure and logit link function tested whether (1) larger males (males with higher crest–back scores or greater body lengths) or higher ranking males were more aggressive than smaller/lower ranking males and (2) whether the frequency of aggression was higher on mating days than on nonmating days. The analyses had one data point per focal male per day (focal animal follows conducted on the same male and day were summed). The response variable was the number of male–male aggressive interactions initiated by the focal male, and focal duration was included as an offset term (log-transformed). We included four test predictors in the model: the two body size variables (crest–back score and body length), dominance rank (on the day of the focal animal sampling period) and whether it was a mating day or not. We did not include interactions between the first three predictors and mating day due to the already high model complexity. We included the age of the focal male and age squared as control variables. The number of males in the group was included to account for variation in opportunities for male–male aggression to occur. Male ID, group ID and group composition were included as random effects.

Probability of contact aggression per male

The second GLMM, a logistic model, tested whether larger/higher ranking males had a higher probability of using contact aggression over noncontact aggression than smaller/lower ranking males and whether this effect was stronger on mating days than on nonmating days. Thus, the response variable indicated whether the aggressive interaction (the data point) comprised contact (1) or noncontact (0) aggression. We included the same test predictors as in the previous model, as well as three two-way interactions of crest–back score, body length and dominance rank with whether it was a mating day or not. We included these two-way interactions to test the hypothesis that the effects of body size and dominance rank were stronger on mating days than on nonmating days. Age, age squared and a temporal autocorrelation term were included as control variables in addition to the same random effects as above.

Frequency of aggression per dyad

The third GLMM with Poisson error structure and log link function tested whether the frequency of aggression was higher between males close in rank or body size than males with larger asymmetries in these two variables. The analysis had one data point per potentially interacting male per dyad combination involving the focal male per day and group (i.e. if male A was one of three males in a group (A, B and C), the analysis had four data points: A–B; A–C; B–A; C–A). Observed dyads per focal male were summed per day. The response was then the number of aggressive interactions that occurred between each dyad, while accounting for the direction of the aggressive interaction (the first male in a dyad is the potential aggressor and the second is the potential recipient). We included the focal duration per dyad per day as an offset term (log-transformed). The test predictors were the relative difference in crest–back score, body length and dominance rank (on the day of the focal animal sampling period) of each dyad (the first individual in the dyad minus the second). We also included the square of these terms, because we expected similar matched dyads (with asymmetries around 0) to exhibit higher frequencies of aggression than unevenly matched dyads (inverse U-shaped curve). We included a variable for whether it was a mating day or not, but we did not include interaction terms between each predictor and mating day due to the already high model complexity. As control variables we included dyadic relatedness, dyadic asymmetry in age and the number of males in the group. Random effects included the

potential aggressor ID, the potential recipient ID, dyad ID, group ID and group composition.

Probability of contact aggression per dyad

The fourth GLMM, a logistic model, tested whether males close in rank or body size had a higher probability of using contact as opposed to noncontact aggression. The response variable indicated whether the aggressive interaction (the data point) was contact (1) or noncontact (0) aggression. The test predictors were the relative differences between the crest–back score, body length and dominance rank of the aggressor and that of the recipient. We expected similar matched dyads (relative differences of around 0) to exhibit higher probabilities of contact aggression than unevenly matched dyads (inverse U-shaped curve). Accordingly, we included squared terms of these three test predictors in the model. We also included whether it was a mating day or not. In addition, we included six two-way interactions between crest–back score, body length and dominance rank, and their respective squared terms, with whether it was a mating day or not, to explicitly test whether the effect of these test predictors on the probability of contact aggression was stronger on mating days than on nonmating days. We included dyadic relatedness, the asymmetry in age and a temporal autocorrelation term as control variables. Random effects were the same as in the previous model.

Ethical Note

This research involved noninvasive work with wild nonhuman primates. All work was done in accordance with guidelines of the Rwanda Development Board and Rwanda Ministry of Education and adhered to all laws of Rwanda.

RESULTS

Body Size and Dominance Rank

Crest–back score correlated positively with average dominance rank in the seven multimale groups (glmmTMB, estimate \pm SE: 1.116 ± 0.336 , $Z = 3.326$, $P < 0.001$; Fig. 1). The alpha male had the largest crest–back score in six of the seven groups, while in 28 of the 38 dyads (74%) the male with the higher crest–back score was higher ranking. Body length also correlated positively with average dominance rank, but this effect was over seven times weaker than the effect of crest–back score and not statistically significant (glmmTMB, estimate \pm SE: 0.158 ± 0.278 , $Z = 0.568$, $P = 0.568$; Fig. 2). To ensure that these results were not driven by young males that had not yet reached full body size, we repeated this analysis after excluding these males. Males reach full back breadth and 98% of crest height by 16.7 years and 98% of body length by 13.1 years (Galbany et al., 2017). When we excluded all males younger than 16.7 years from the analysis ($N = 10$) the relationships between crest–back score and dominance rank (glmmTMB, estimate \pm SE: 1.125 ± 0.324 , $Z = 3.473$, $P < 0.001$) and body length and dominance rank (estimate \pm SE: 0.182 ± 0.292 , $Z = 0.622$, $P = 0.534$) remained similar. Despite both crest–back score, and body length being correlated positively with dominance rank, we were able to include them in the subsequent analyses without leading to collinearity issues (see Appendix Statistical analysis: additional information).

Body Size, Alpha Male Tenure Length and Number of Adult Females

The median alpha male tenure length was 4.9 years ($N = 10$; range 1.6–20.6). Crest–back score correlated positively with alpha male tenure length (LM, estimate \pm SE: 0.567 ± 0.214 , $T = 2.652$,

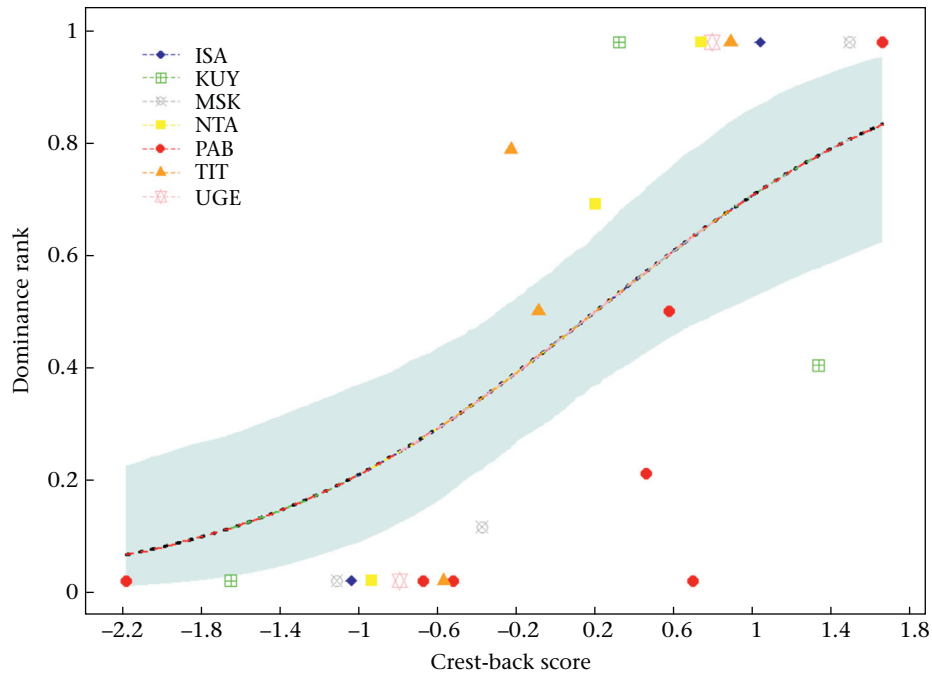


Figure 1. Relationship between crest–back score and dominance rank of 24 males in the seven multimale groups. Dominance rank was averaged across the study period and standardized between 0 (lowest rank) and 1 (highest rank). Crest–back score was centred around the group mean crest–back score (see text). Larger crest–back scores refer to larger absolute values. The random intercept of group had a very small variance meaning that the model line for each group was essentially the same. The shaded area represents the 95% confidence intervals, with all the other variables in the model being at their mean.

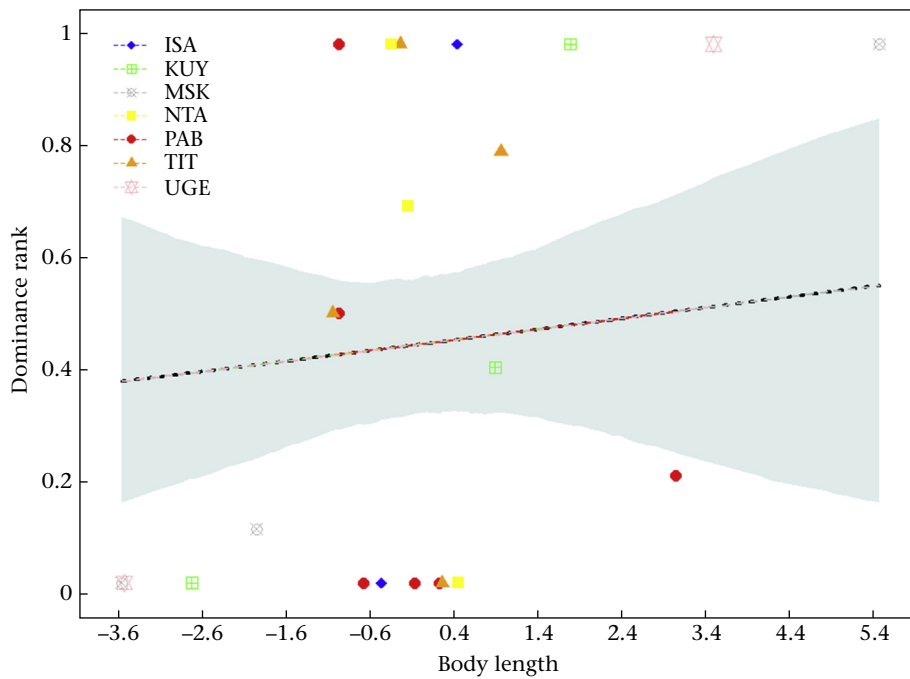


Figure 2. Relationship between body length and dominance rank of 24 males in the seven multimale groups. Dominance rank was averaged across the study period and standardized between 0 (lowest rank) and 1 (highest rank). Body length was centred around the group mean body length (see text). Larger body lengths refer to larger absolute values. The random intercept of group had a very small variance meaning that the model line for each group was essentially the same. The shaded area represents the 95% confidence intervals, with all the other variables in the model being at their mean.

$P = 0.012$; $R^2 = 0.47$; Fig. 3a). An increase in crest–back score by one standard deviation was associated with an increase of 76% in tenure length. Body length also correlated positively with alpha male tenure length, but this effect was around six times smaller than the effect of crest–back score, it was associated with large

statistical uncertainty and not statistically significant (LM, estimate \pm SE: 0.090 ± 0.291 , $T = 0.310$, $P = 0.730$; $R^2 = 0.09$; Fig. 3b). The median number of adult females per alpha male tenure was 3.5 (range 2.1–14.3). Alpha crest–back score correlated positively with the average number of adult females per tenure (LM, estimate \pm SE:

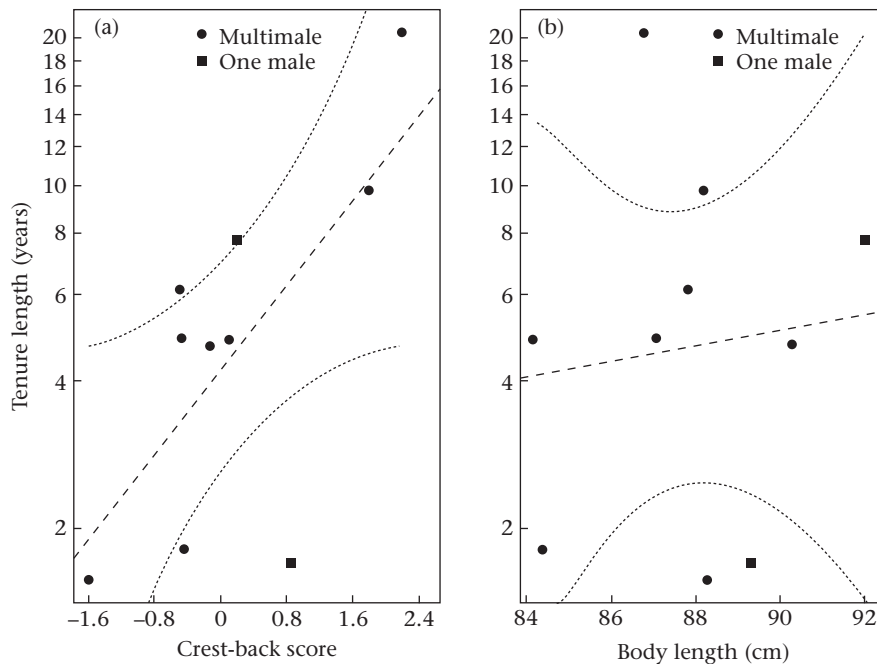


Figure 3. Relationship between alpha male tenure length and (a) crest–back score and (b) body length. Y-axes are on a log scale. Each point refers to an alpha male tenure period ($N = 10$). The dashed lines are model lines, and the two dotted lines are 95% confidence intervals.

0.387 ± 0.120 , $T = 3.221$, $P = 0.004$; $R^2 = 0.48$; Fig. 4a). An increase in crest–back score by one standard deviation resulted in an increase of 47% in the number of adult females. Body length was weakly negatively correlated with the average number of adult females per tenure; however, the standard error was more than twice as large as the estimate and this effect was not statistically significant (LM, estimate \pm SE: -0.069 ± 0.181 , $T = -0.384$, $P = 0.669$; $R^2 = 0.03$; Fig. 4b).

Frequency of Aggression per Male

We recorded 774 adult male–male aggressive interactions, 265 (34%) during focal animal sampling and 509 (66%) during ad libitum observations. Of these, 139 (18%) involved contact aggression and 635 (82%) involved noncontact aggression. Male–male aggression occurred on average 0.09 times/h (range 0–0.27 per male). Crest–back score (GLMM, estimate \pm SE: 0.472 ± 0.166 , $P = 0.003$; Fig. 5a), but not dominance rank or body length, significantly influenced the frequency of aggression, which was also significantly higher on mating days than on nonmating days (GLMM, estimate \pm SE: 0.776 ± 0.288 , $P = 0.048$; see Appendix Table A5 for further details of GLMM results).

Probability of Contact Aggression per Male

The probability that a male used contact aggression towards another male was not significantly correlated with crest–back score, body length, dominance rank or whether it was a mating day or not (comparison of a model comprising these variables and a model with these variables excluded; $\chi^2_7 = 9.401$, $P = 0.225$).

Frequency of Aggression per Dyad

The frequency of aggression increased significantly as the crest–back score of the potential aggressor increased relative to the potential recipient (GLMM, estimate \pm SE: 0.485 ± 0.173 , $P = 0.006$;

Fig. 5b). Moreover, the frequency of aggression was significantly higher when the asymmetry in dominance rank approached zero (GLMM, estimate \pm SE: -0.823 ± 0.152 , $P < 0.001$; inverse U-shaped relationship; Fig. 5c). The magnitude of the body length difference between males did not significantly influence the frequency of aggression. See Appendix Table A6 for further details of GLMM results.

Probability of Contact Aggression per Dyad

The influence of the magnitude of the rank difference between males on the probability of contact aggression depended on whether it was a mating day or not (GLMM, interaction between the asymmetry in dominance rank squared and mating day: estimate \pm SE: -1.039 ± 0.424 , $P = 0.004$; Fig. 6). On mating days, the probability of contact aggression was significantly higher between similar ranking males and when the aggressor was slightly higher ranking relative to the recipient (Fig. 6a). On nonmating days, the probability of contact aggression was significantly higher when the aggressor was higher ranking than the recipient (Fig. 6b). The magnitude in crest–back score and body length difference between males did not significantly influence the probability of contact aggression. See Appendix Table A7 for further details of GLMM results.

DISCUSSION

Body Size and Dominance Rank

Our findings provide support for a key prediction of sexual selection theory, that large body size helps males acquire high dominance rank and reproductive success. This pattern is commonly found across a wide range of animals (Andersson, 1994; Clutton-Brock, 2017; Haley, Deutsch, & Le Boeuf, 1994; McElligott et al., 2001; Pelletier & Festa-Bianchet, 2006; Setchell, Wickings, & Knapp, 2006; but see: ; Feh, 1990; Kitchen et al., 2003; Lawler et al., 2005; Lidgard et al., 2005; Neumann et al., 2010; Pusey et al., 2005;

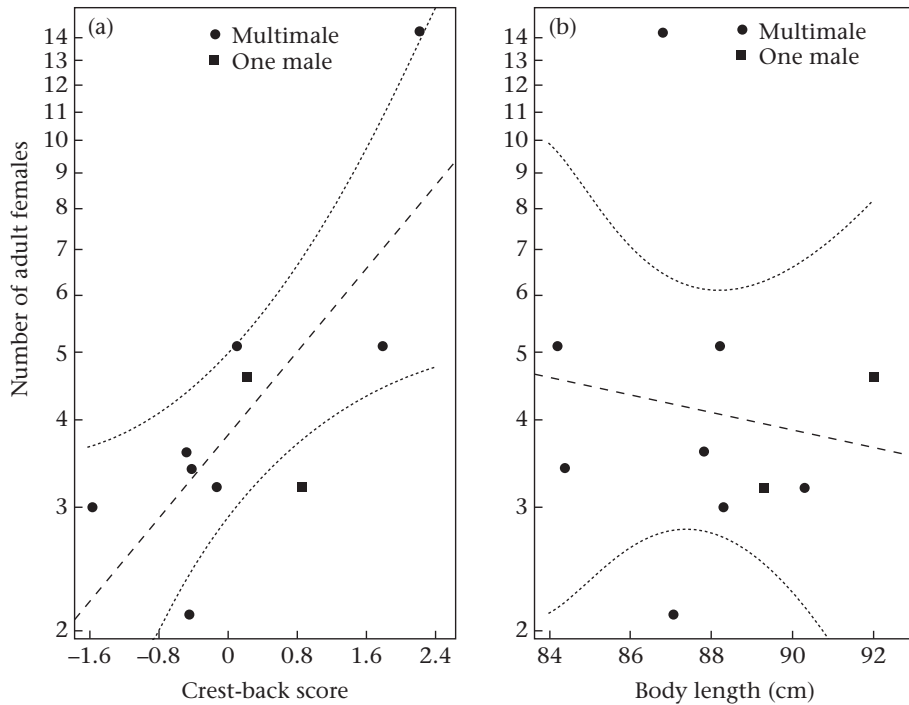


Figure 4. Relationship between number of females and (a) crest–back score and (b) body length. Y-axes are on a log scale. Each point refers to an alpha male tenure period ($N = 10$). The dashed lines are model lines, and the two dotted lines are 95% confidence intervals.

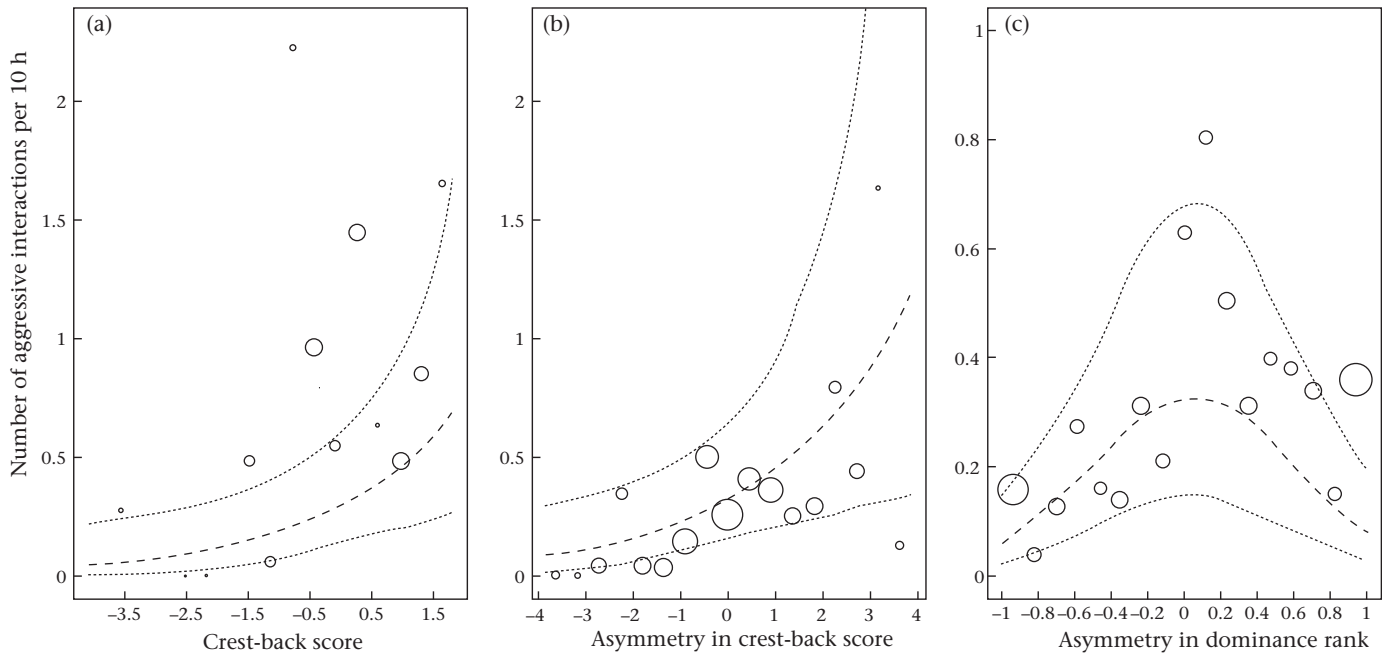


Figure 5. Relationship between the frequency of aggression and (a) crest–back score, (b) asymmetry in crest–back score and (c) asymmetry in dominance rank. Larger crest–back scores refer to larger absolute values. Asymmetries of around zero indicate that the two males had similar crest–back scores/dominance rank, negative asymmetries indicate that the aggressor had a smaller crest–back score/lower rank than the recipient and positive asymmetries indicate that the aggressor had a larger crest–back score/higher rank than the recipient. The area of the circles depicts sample size ($N_a = 3282$ focal animal sampling periods; N_b and $N_c = 11\,404$ dyadic observation periods per focal day). The dashed lines are the model lines, and the two dotted lines are 95% confidence intervals with all the other variables in the models being at their mean.

Spong et al., 2008). However, it remains understudied in permanently group-living mammals (Bergeron et al., 2010; Plavcan, 2004), in which other factors may play a role due to the long-term, cohesive nature of social groups. We have shown that crest–back score, a composite measure of two positively correlated

variables (crest height and back breadth), is strongly correlated with male dominance rank in multimale groups of mountain gorillas (Fig. 1). However, the lack of a 1:1 correlation between crest–back score and dominance rank highlights that traits other than body size also contribute to a male's rank.

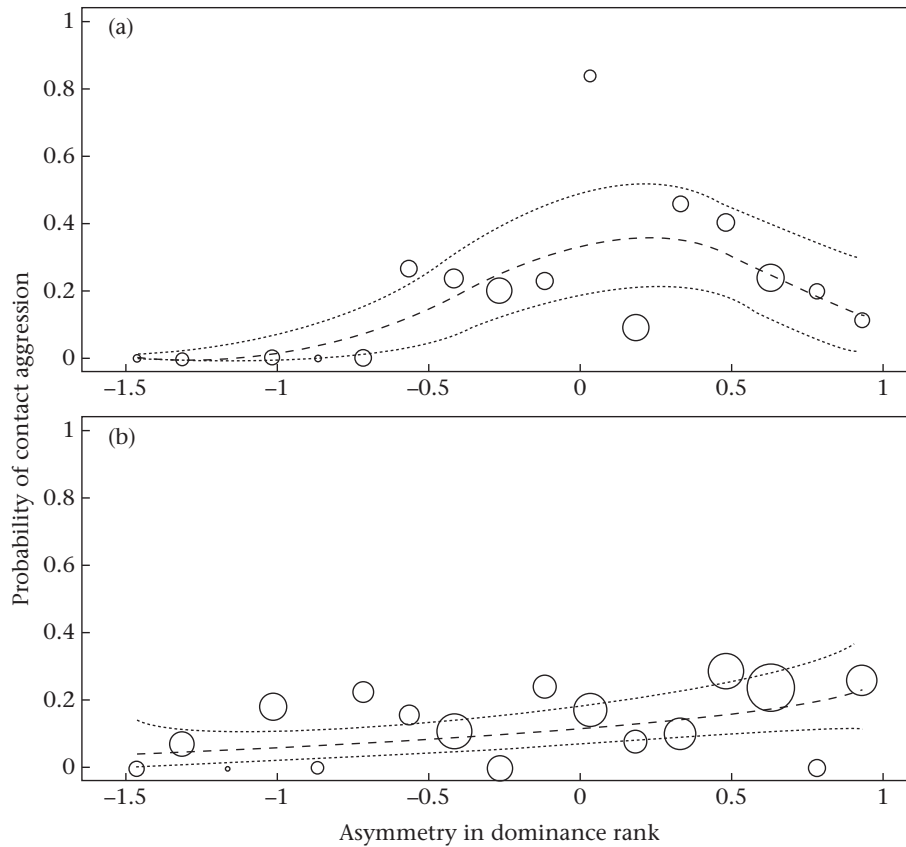


Figure 6. Relationship between the probability of contact aggression and asymmetry in dominance rank, displayed for (a) mating days and (b) nonmating days. Asymmetries in rank of around zero indicate that both males had similar ranks, while negative asymmetries in rank indicate that the aggressor was lower ranking than the recipient and positive asymmetries indicate that the aggressor was higher ranking than the recipient. Note that the asymmetry in dominance rank was centred around the group mean asymmetry in rank, which can lead to values exceeding the range of -1 to 1 (see Methods). The size of the circles depicts sample size ($N = 774$). The dashed lines are the model lines, and the dotted lines are 95% confidence intervals with all the other variables in the model being at their mean.

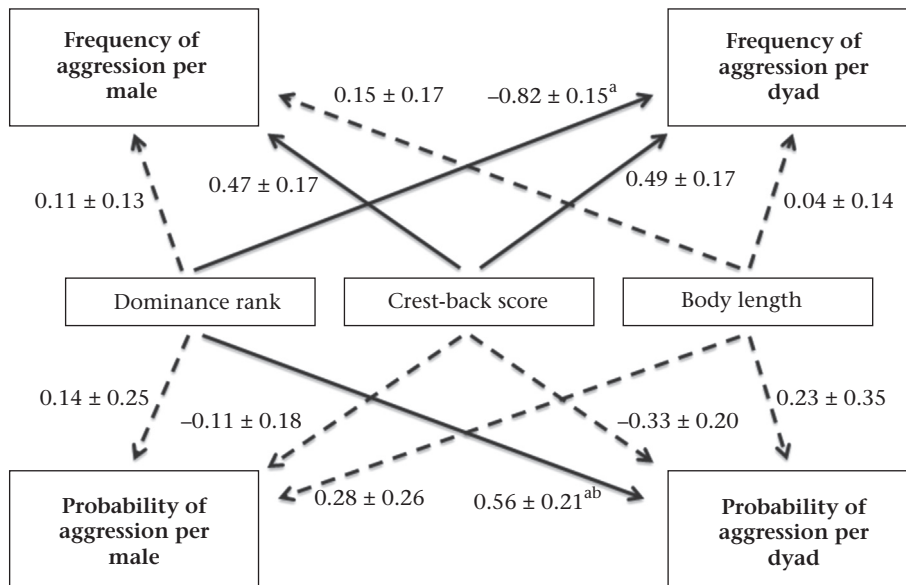


Figure 7. Path diagram depicting the four aggression models (response variables in bold) and the three main test predictors: dominance rank, crest–back score and body length. Solid arrows depict significant effects and dashed arrows depict nonsignificant effects. Estimates with standard errors are shown for each relationship. In the two dyad models the relative differences in dominance rank, crest–back score and body length between dyads were tested. Superscript ^a indicates inverse U-shaped relationships; ^b indicates dominance rank squared was involved in an interaction with mating day (see text).

Body length was only weakly related to dominance rank (Fig. 2) and was not significantly correlated with alpha male tenure length (Fig. 3b) or the number of adult females in the group (Fig. 4b); it also had little explanatory power in any of the aggression analyses (Fig. 7). In western lowland gorillas, body length was found to correlate positively with number of adult females per group, but this trait was not as important as crest size in predicting male reproductive success (Breuer et al., 2012). Both crest height and back breadth are likely to reflect muscle mass, fat tissue and bone structure and therefore these traits may better indicate body condition and strength than body length, which is predominantly a function of bone length. Crest size has been suggested to reflect temporal muscle size and therefore bite force as well as energy reserves and overall health status (Balolia, Soligo, & Wood, 2017; Breuer et al., 2012; Caillaud et al., 2008). Crest height and back breadth also show larger between-male variation (Appendix Table A8) and higher sexual dimorphism than body length (Galbany et al., 2017), suggesting that crest height and back breadth are under stronger selection and play a more important role in male–male competition. These results are similar to findings in humans: upper body size (and its correlates) was perceived as a better predictor of competitive ability than body height in men (Sell et al., 2009). Lastly, if crest height and back breadth are indeed indicators of body condition, it is possible that attaining (and losing) alpha male status may lead to increases (and decreases) in the size of these traits, similar to findings in male mandrills, *Mandrillus sphinx*, for example (Setchell & Dixson, 2001). Further work is needed to elucidate whether these traits change over time in adult male mountain gorillas.

Body Size, Alpha Male Tenure Length and Number of Adult Females

Crest–back score correlated positively with alpha male tenure length, indicating that large body size assists males in retaining as well as attaining high rank via superior fighting ability (Fig. 3a). Few studies have been able to examine alpha male tenure length in males of known body size (or mass). Our findings are similar to those reported in elephant seals, *Mirounga angustirostris* (Modig, 1996) and alpine marmots, *Marmota marmota* (Lardy, Cohas, Desouhant, Tafani, & Allainé, 2012), but they contrast with results from meerkats, *Suricata suricatta* (Spong et al., 2008). However, as body size does not significantly correlate with dominance rank in meerkats, we would not expect it to significantly influence alpha male tenure length. Aside from body size, demographic factors such as the number of adult males and females in social groups have also been shown to influence alpha male tenure length (Lukas & Clutton-Brock, 2014; Setchell et al., 2006; Spong et al., 2008), but due to the relatively small sample size of complete tenures, this could not be examined in the current study.

Alpha male crest–back score correlated significantly with the number of adult females per group (Fig. 4a), which is similar to findings of a positive relationship between body size and number of adult females in one-male groups of western lowland gorillas (Breuer et al., 2012; Caillaud et al., 2008) and other polygynous mammals (Clutton-Brock, Albon, & Guinness, 1988; Le Boeuf, 1974). Female gorillas transfer between social groups multiple times in their lives, probably indicating a preference for groups of a certain size or for males with particular traits (Sicotte, 2001). Therefore, our finding of large males leading groups with more females may reflect female preference for large males which are better able to provide protection against infanticidal males and/or have higher genetic quality than smaller males (Robbins et al., 2013). The number of adult females in the group has been shown to correlate positively with alpha male siring rates in this population (Robbins et al., 2014). Combining these results with previous findings of

alpha males siring the majority of offspring in multimale groups (Bradley et al., 2005; Vigilant et al., 2015), we can expect a positive correlation between body size and lifetime reproductive success as has also been found in red deer, *Cervus elaphus* (Clutton-Brock et al., 1988). While data on body size and lifetime reproductive success remain scarce, a number of studies have found positive correlations between body size and short-term reproductive success in Soay sheep, *Ovis aries* (Preston, Stevenson, Pemberton, & Wilson, 2001), elephant seals (Haley et al., 1994), mountain goats, *Oreamnos americanus* (Mainguy, Côté, Festa-Bianchet, & Coltman, 2009) and eastern grey kangaroos, *Macropus giganteus* (Miller, Eldridge, Cooper, & Herbert, 2010).

Body Size, Dominance Rank and Patterns of Aggression in Multimale Groups

The frequency of aggression among males was low, as previously observed (Robbins, 1996; Sicotte, 1994; Stoinski et al., 2009), which is likely to be a consequence of stable dominance hierarchies (Rowell, 1974). Furthermore, aggressive interactions among males for access to matings occurred relatively infrequently because females are sexually receptive for only 1–2 days per month, typically conceive within 6 months of oestrous cycles and have 3 years of lactational amenorrhoea without mating per 4-year interbirth interval (Robbins, 2011), and groups contain relatively few females (approximately 3.5; this study). The majority of contests involved noncontact aggression, which probably reflects the high costs of contact aggression and is expected in long-lived, large animals (Port & Cant, 2013). However, some higher intensity contact aggression may occur to allow individuals to monitor changes in fighting ability over time. Whereas aggression was used strategically, with males enforcing and challenging dominance relationships on days when reproductive opportunities were likely to occur, males concurrently adopted a low-cost strategy by primarily targeting males considerably smaller than themselves.

The frequency of aggression was significantly related to both male crest–back score (Fig. 5a and 7) and the magnitude of the crest–back score difference between males (Fig. 5b), with large males predominantly directing aggression towards much smaller ones. This finding went against our hypothesis of increased aggression between similar-sized males. The costs associated with aggression, in terms of the risk of injury, can be expected to be significantly lower when targeting much smaller individuals rather than similar-sized males. Large males may also gain fitness benefits by aggressively punishing smaller ones (Clutton-Brock & Parker, 1995). In addition, large males may direct aggression against smaller males, to force them to disperse (and reduce within-group male–male competition). However, a previous study on mountain gorillas did not find that young males received increased levels of aggression in the months preceding dispersal (Stoinski et al., 2009). Furthermore, smaller males may sometimes initiate aggression with larger males (Fig. 5b), but only infrequently to avoid potentially costly contests with larger males that they are unlikely to defeat. The probability of contact aggression was not significantly related to either individual crest–back score or the difference in crest–back score between contestants, which is unsurprising given that large males predominantly targeted much smaller males in aggression, and hence were unlikely to need to resort to higher intensity contact aggression to win contests.

The frequency of aggression was not significantly related to individual dominance rank but was significantly related to the magnitude of the rank difference between males, with increased frequency of aggression among males close in rank (Figs 5c and 7). The probability of contact aggression showed a similar pattern, although the effects were dependent on whether it was a mating

day or not (Fig. 6). On mating days, the probability of contact aggression was highest between males close in rank and when the aggressor was slightly higher ranking relative to the recipient, but on nonmating days contact aggression was predominantly directed down the dominance hierarchy, from higher ranking males towards lower ranking ones. Higher ranking males probably reinforce their dominant position over males ranking just below them in the dominance hierarchy, whereas lower ranking males probably attempt to challenge the rank position of males just above them in the hierarchy. These rank conflicts intensified on matings days, which is likely to reflect competition for receptive females.

That lower ranking males directed some aggression at higher ranking ones is surprising, although this occurred less often when higher intensity contact aggression was used. Lower ranking males are likely to be faced with a trade-off between attempting to improve their rank and entering into costly contests with other individuals with superior fighting ability. We found no evidence for a positive relationship between dominance rank and either frequency or intensity of aggression. The highest-ranking males in a group may not need to use frequent aggression to gain access to resources as lower ranking males are likely to avoid them (Holekamp & Strauss, 2016). Further work examining male spatial association patterns as well as the proximate mechanisms that drive these are needed to test this hypothesis.

Our findings of increased frequency and intensity of contests among similar ranking males is in line with game theory predictions (Parker, 1974), and has been found in baboons, *Papio ursinus* (Kitchen et al., 2003) and several species of ungulates (Jennings et al., 2006; McElligott et al., 1998), but contrasts with the pattern we found for crest–back score where large positive asymmetries between males predicted the results. This is likely to be explained by dominance rank reflecting a composite of body size (perhaps being the most important component), body condition, fighting experience and other factors, and is thus a better proxy for RHP than body size alone. Allocating energy to growth of secondary sexual characteristics such as large body size may impose energetic trade-offs with investing in somatic maintenance and body condition (Clutton-Brock, 2017; Thompson & Georgiev, 2014). The relative investment in these life history components, growth of body size and maintenance of body condition, is likely to be influenced by the degree of male–male competition driven by the number of reproductive opportunities across time and space, and further constrained by food resource availability (Lukas & Clutton-Brock, 2014). Evidence for the survival costs of developing secondary sexual characteristics has started to accumulate, but further work is needed, especially estimates of lifetime reproductive success (Clutton-Brock, 2017).

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Appendix

Photogrammetry Error

We assessed measurement error in three ways: (1) within-photo error, by comparing the measurements obtained from the same photos ($N = 20$) on three different occasions without consulting previous measurements; (2) within-individual error, by comparing the measurements obtained from different photos of the same trait and male; (3) interobserver error, by comparing measurements obtained by E.W. and J.G. using separate laser devices on the same males ($N = 15$ males; photographed at similar times). The mean errors reported here are similar to those reported elsewhere (Barrickman, Schreier, & Glander, 2015; Lu, Bergman, McCann, Stinespring-Harris, & Beehner, 2016; Rothman et al., 2008). The mean coefficients of variation (CVs) for the within-photo, within-individual and interobserver errors were around 1% with the exception of the within-individual error for crest height, which varied slightly more than the other two traits (Table A1).

Photogrammetry Validation

We directly compared the photogrammetry measurements from nine males that died during the study with measurements taken from them directly during necropsies. These comparisons revealed low errors for body length (0.9%), but slightly higher errors for crest height (8.7%) (Table A2). See Galbany et al. (2016, 2017) for further discussion on why measurement errors may be slightly higher for crest height than for body length or back breadth.

Principal Component Analysis

We visually inspected whether the three traits had approximately symmetric distributions and their relationships were linear. The PCA was justified as shown by the Kaiser–Meyer–Olkin measure of 0.57 and Bartlett's test of sphericity ($\chi^2_3 = 22.932$, $P < 0.001$; McGregor, 1992).

Statistical Analysis: Additional Information

Model assumptions and model stability

We checked for under/overdispersion in the negative binomial (formerly a Poisson model but the dispersion parameter was a little high at 1.25; we therefore opted for a negative binomial model instead) and Poisson models. The dispersion parameters were close to the ideal value of 1: 0.97 and 1.06 for the frequency of aggression per male and per dyad models, respectively. We checked various diagnostics of model validity and stability in the LMs (DFBetas, DFFits and leverage; distribution of residuals plotted against fitted values). All the assumptions were met. In the GLMMs we checked for collinearity among predictor variables by examining variance inflation factors derived from models without random effects, squared terms or interactions using the 'vif' function of the 'car' package (Fox & Weisberg, 2011). The maximum vif in all models was 2.7; crest–back score correlated positively with dominance rank, although this correlation was not overly high, and hence it was possible to include both variables in the analyses without leading to collinearity issues. In addition, we checked for model stability by rerunning the models after excluding levels of each random effects factor one at a time and comparing the estimates derived from these models with the estimates from the original full model. No stability issues were found. All continuous predictor variables were z-transformed (to a mean of 0 and standard deviation of 1).

Random effect of date nested in group

Because on some days multiple focal animal sampling periods were conducted on the same group in the two frequency of aggression models, date nested in group should be included as a random effect (to avoid pseudoreplication of observation day). The inclusion of this random effect, however, was problematic in terms of model stability due to a combination of the many zeros in the response (focal animal sampling periods with no aggression) and its highly skewed nature. We therefore dropped this random effect from these two models. However, as the consequences of this are not entirely clear, the results from these two models should be viewed with caution. Pseudoreplication of date nested in group may result in slightly elevated type 1 errors (overly anti-conservative P values) for test predictors that vary between date nested in group and type 1 or type 2 errors (false-negative findings) for test predictors that vary within date nested in group. However, we are confident that dropping this random effect is unlikely to have a significant effect on the results. Observation days with more than one aggressive interaction were rare (0.6% and 3.4% for the frequency of aggression per male and dyad model, respectively); thus, it is highly unlikely that any given day would have had a very different contribution to the results compared to other days. Therefore, including date nested in group as a further random effect is unlikely to have had a significant effect on the results.

Additional control variables: dyadic relatedness and male age

We included dyadic relatedness in the two dyadic models to control for the possibility that more related dyads were involved in fewer (or less intense) aggressive interactions than less related dyads. Pedigree relatedness was used to classify each male–male dyad as unrelated (if the two males had a different mother and a different father; $N = 11$), half-siblings (if the males had the same mother or the same father; $N = 15$) or a combination of father–son ($N = 4$) and full siblings (if the two males had the same mother and the same father; $N = 1$). Paternity is known from Bradley et al. (2005), Vigilant et al. (2015) and Vigilant, Robbins, Eckardt, and Stoinski (2017). Also, age and the asymmetry in age between the

aggressor and the recipient in the two dyadic models were included as control variables because males of different ages may have different propensities of aggressiveness.

Temporal autocorrelation

We accounted for potential autocorrelation in the residuals (residuals of data points close in time being more similar to each other than residuals of data points further apart) in the two contact aggression models using the same method as explained in Fürtbauer, Mundry, Heistermann, Schülke, and Ostner (2011) and Wright et al. (2015) and included it as a control variable. Temporal autocorrelation terms were unlikely to be meaningful in the two frequency of aggression models due to the high occurrence of zeroes in the response and were not included.

Full null model comparisons and computation of P values

In the models comprising more than one predictor, we compared each model to a corresponding null model (with the test

predictors excluded) using likelihood ratio tests, before examining the significance of the individual test predictors, which was only conducted when this comparison was significant. *P* values for the individual predictors were computed using likelihood ratio tests comparing a full model with a reduced model not comprising the test variable (excluded one at a time).

Confidence intervals and random slopes

We determined 95% confidence intervals using the function 'simulate.glmTMB' of the glmTMB package (Brooks et al., 2017) and the 'bootMer' of the lme4 package (Bates et al., 2015). As much as the data allowed, we included random slopes for the effects of the predictors on the response to vary between levels of each random effect (Barr, Levy, Scheepers, & Tily, 2013; Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017; Schielzeth & Forstmeier, 2009; Table A4). In the glmTMB model we included the random slopes for the effects of crest–back score and body length on dominance rank to vary between levels of group ID.

Table A1

Within-photo, within-individual and interobserver measurement error

Morphological trait	Mean within-photo CV (%)	Mean within-individual CV (%)	Mean interobserver error CV (%)	Mean interobserver error (%)
Crest height	1.1 (0.3–2.0)	4.5 (2.1–6.6)	1.5 (0.4–3.5)	2.1 (0.6–4.8)
Body length	0.6 (0.1–1.1)	1.2 (0.3–2.9)	0.8 (0.0–2.2)	1.1 (0.0–3.1)
Back breadth	0.8 (0.2–1.4)	1.4 (0.1–2.9)	0.9 (0.0–2.8)	1.3 (0.0–4.1)

Numbers in parentheses are minimum and maximum values. CV: coefficient of variation. Interobserver error was calculated by dividing the absolute difference between E.W.'s measurement and J.G.'s measurement by E.W.'s measurement, multiplied by 100.

Table A2

Comparison of measurements obtained from photogrammetry with those obtained during necropsy

Silverback	Method	Crest height (cm)	Body length (cm)
ISA	PG	17.6	88.2
	Necropsy	16.5	90.0
	% Error	6.7	2.0
TRK	PG	15.4	88.3
	Necropsy	15.0	88.5
	% Error	2.7	0.2
GIR	PG	17.1	89.3
	Necropsy	15.0	89.5
	% Error	14.0	0.2
VUB	PG	17.2	89.4
	Necropsy	15.5	88.0
	% Error	11.0	1.6
KRB	PG	18.4	90.8
	Necropsy	16.0	91.0
	% Error	15.0	0.2
RAN ^a	PG	15.8	88.4
	Necropsy	18.0	88.0
	% Error	12.2	0.5
BWE ^a	PG	17.5	91.8
	Necropsy	16.0	91.0
	% Error	9.4	0.9
UGE ^a	PG	15.4	88.4
	Necropsy	14.5	87.0
	% Error	6.2	1.6
WAG ^a	PG	14.2	80.3
	Necropsy	14.0	81.0
	% Error	1.4	0.9
	Mean error %	8.7	0.9

Rigor mortis prevented us from measuring back breadth during necropsy. PG: photogrammetry. % Error was calculated by dividing the absolute difference between the photogrammetry and necropsy measurements by the necropsy measurement, multiplied by 100. Mean error % refers to the mean error across all males for body length and crest height.

^a Taken from Galbany et al. (2017).

Table A3
Summary of the four statistical tests examining patterns of aggression in multimale groups

Model	Response	Data point and sample size	Test predictors	Control predictors	Random effects
Frequency of aggression per male	Number of aggressive interactions initiated (negative binomial)	Focal period $N = 3282$ (2927 h)	Crest–back score Body length Dominance rank Mating day	Age Age squared Number of males in group Focal duration (offset)	Male ID ($N = 22$) Group ID ($N = 7$) Group composition ($N = 14$)
Probability of contact aggression per male	Contact vs noncontact aggression (binomial)	Aggressive interaction $N = 774$		Age Age squared Temporal autocorrelation	Male ID ($N = 22$) Group ID ($N = 7$) Group composition ($N = 14$)
Frequency of aggression per dyad	Number of aggressive interactions (Poisson)	Dyadic focal period $N = 11404$ (12722 h)	Δ Crest–back score ^a Δ Body length ^a Δ Dominance rank ^a Mating day	Δ Age Relatedness Number of males in group Dyadic focal duration (offset)	Aggressor ID ($N = 22$) Recipient ID ($N = 22$) Dyad ID ($N = 54$) Group ID ($N = 7$) Group composition ($N = 14$)
Probability of contact aggression per dyad	Contact vs noncontact aggression (binomial)	Aggressive interaction $N = 774$		Δ Age Relatedness Temporal autocorrelation	Aggressor ID ($N = 22$) Recipient ID ($N = 24$) Dyad ID ($N = 56$) Group ID ($N = 7$) Group composition ($N = 14$)

Δ : the relative difference in each variable between the (potential) aggressor and (potential) recipient.

^a Squared terms were also included in the model. Interaction terms between crest–back score, body length and dominance rank with mating day were included in the two binomial models (as well as the squared terms in the probability of contact aggression per dyad model).

Table A4
Random slope structure of the four aggression models

Model	Fixed effect	Random effect
Frequency of aggression per male	Crest–back score Body length Dominance rank Mating day	Group ID Group ID Group ID; Group composition
Probability of contact aggression per male	Crest–back score Body length Dominance rank Mating day Age Age squared Crest–back score*mating day Body length*mating day Dominance rank*mating day	Group ID; Group composition; Focal ID Group ID Group ID Group ID ; Group composition Group ID; Group composition Group ID; Group composition Group ID; Group composition
Frequency of aggression per dyad	Δ Crest–back score Δ Crest–back score squared Δ Body length Δ Body length squared Δ Dominance rank Δ Dominance rank squared Δ Age Mating day	Group ID; Group composition Group ID; Group composition Group ID; Group composition Group ID; Group composition Group ID; Group composition; Aggressor; Recipient; Dyad Group ID; Group composition; Aggressor; Recipient; Dyad Group ID; Group composition; Aggressor; Recipient
Probability of contact aggression per dyad	Δ Crest–back score Δ Crest–back score squared Δ Body length Δ Body length squared Δ Dominance rank Δ Dominance rank squared Δ Age Mating day Δ Crest–back score*mating day Δ Crest–back score squared*mating day Δ Body length*mating day Δ Body length*mating day Δ Dominance rank*mating day Δ Dominance rank*mating day	Group ID; Group composition; Aggressor; Recipient Group ID; Group composition; Aggressor; Recipient Group ID; Group composition; Aggressor; Recipient Group ID; Group composition; Aggressor; Recipient Group ID; Group composition; Aggressor; Recipient Group ID; Group composition; Aggressor; Recipient Group ID; Group composition; Aggressor; Recipient; Dyad Group ID; Group composition; Aggressor Group ID; Group composition; Aggressor Group ID; Group composition; Aggressor Group ID; Group composition; Aggressor Group ID; Group composition; Aggressor

We included all possible random slope terms to allow for the effect of each fixed effect on the response to vary between levels of each random effect. Random effects on the same row as each fixed effect indicate that the random slope(s) of the fixed effect within the random effect(s) were included. Final models only included random slope terms with meaningful variance (bold text); random slope terms with zero variance (nonbold text) were dropped from the final models to prevent overcomplex random effects structures. Δ : the relative difference in each variable between the (potential) aggressor and (potential) recipient.

Table A5

The influence of crest–back score, body length, dominance rank, mating day and other variables on the frequency of aggression per male

Predictors	Estimate	SE	CL _{lower}	CL _{upper}	χ^2	df	P
Intercept	−7.619	0.363	−8.371	−6.939			
Crest–back score	0.472	0.166	0.076	0.912	8.636	1	0.003
Body length	0.148	0.238	−0.353	0.641	0.364	1	0.546
Dominance rank	0.114	0.127	−0.235	0.404	0.422	1	0.516
Mating day	0.776	0.288	0.136	1.193	3.924	1	0.048
Age	−0.828	0.283	−1.453	−0.134			
Age squared	0.395	0.136	0.126	0.688	4.753	1	0.029
Number of males	0.130	0.211	−0.397	0.550	0.383	1	0.536

CL: upper and lower confidence limits. Significant test predictors are indicated in bold. Full null model comparison: $\chi^2_4 = 15.588$, $P = 0.004$.**Table A6**

The influence of the asymmetry in crest–back score, body length and dominance rank between the aggressor and the recipient and other variables on the frequency of aggression

Predictors	Estimate	SE	CL _{lower}	CL _{upper}	χ^2	df	P
Intercept	−7.907	0.515	−9.126	−6.94			
Δ Crest–back score	0.485	0.173	0.117	0.867	7.575	1	0.006
Δ Body length	0.037	0.136	−0.251	0.333	0.074	1	0.785
Δ Dominance rank	0.101	0.209	−0.358	0.553			
Δ Dominance rank squared	−0.823	0.152	−1.166	−0.491	26.874	1	<0.001
Mating day	0.489	0.239	−0.117	0.945	2.283	1	0.131
Δ Age	0.304	0.261	−0.231	0.822	1.281	1	0.258
Relatedness: half siblings vs father-son	0.303	0.447	−0.536	1.381	1.747	2	0.417
Relatedness: unrelated vs father-son	0.566	0.435	−0.269	1.577			
Number of males	−0.532	0.185	−0.98	−0.125	6.544	1	0.011

CL: upper and lower confidence limits. Δ: the asymmetry in each variable between the aggressor and recipient. Nonsignificant squared terms were removed from the final model. Significant test predictors are indicated in bold. Full null model comparison: $\chi^2_7 = 37.945$, $P < 0.001$.**Table A7**

The influence of the asymmetry in crest–back score, body length and dominance rank between the potential aggressor and the potential recipient and other variables on the probability of contact aggression

Predictors	Estimate	SE	CL _{lower}	CL _{upper}	χ^2	df	P
Intercept	−2.619	0.552	−4.374	−1.713			
Δ Crest–back score	−0.329	0.200	−0.764	0.112	2.670	1	0.102
Δ Body length	0.279	0.354	−0.465	1.069	0.572	1	0.450
Δ Dominance rank	0.555	0.211	0.173	0.965			
Δ Dominance rank squared	0.024	0.170	−0.303	0.332			
Mating day	1.282	0.430	0.503	2.175			
Δ Age	−0.108	0.218	−0.590	0.338	0.240	1	0.624
Relatedness: half siblings vs father-son	0.605	0.565	−0.362	2.332	2.375	2	0.305
Relatedness: unrelated vs father-son	0.879	0.569	−0.095	2.600			
Temporal autocorrelation	0.371	0.087	0.197	0.572	17.422	1	0.000
Δ Dominance rank*Mating day	0.028	0.321	−0.577	0.828	0.007	1	0.932
Δ Dominance rank squared*Mating day	−1.039	0.424	−2.230	−0.398	8.168	1	0.004

CL: upper and lower confidence limits. Δ: the asymmetry in each variable between the aggressor and recipient. Nonsignificant interactions and squared terms were removed from the final model. Significant test predictors are indicated in bold. Full null model comparison: $\chi^2_{13} = 32.304$, $P < 0.002$.**Table A8**

Mean, range and coefficients of variation (CV) among males for the three morphological traits

Trait	Mean	Range	CV (%)
Crest height	16.4	14.4–18.7	7.9
Back breadth	59.2	54.6–65.0	4.9
Body length	87.7	80.8–96.5	3.3

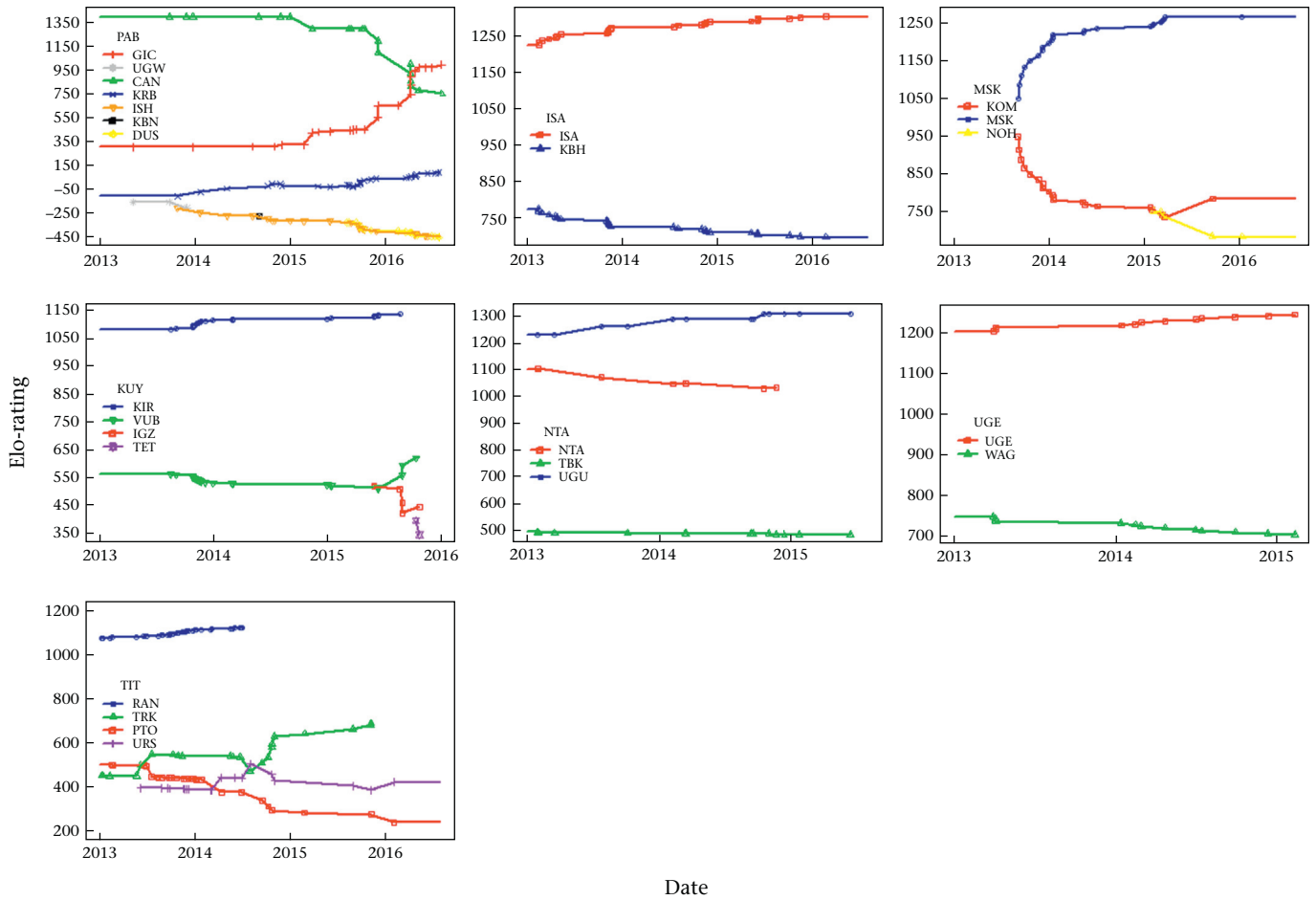


Figure A1. ELO-ratings for each group between January 2013 and July 2016. ELO-ratings were calculated using long-term dominance interactions dating back to the formation of each group, but data are only shown for 2013–2016. Each symbol denotes a male and each data point represents an interaction with lines between data points representing the change in ELO-rating for the two interacting males.