

UC Davis

UC Davis Previously Published Works

Title

Predictors of insubordinate aggression among captive female rhesus macaques

Permalink

<https://escholarship.org/uc/item/4f0475kd>

Journal

American Journal of Biological Anthropology, 164(3)

ISSN

0002-9483

Authors

Seil, Shannon K
Hannibal, Darcy L
Beisner, Brianne A
et al.

Publication Date

2017-11-01

DOI

10.1002/ajpa.23296

Peer reviewed



Published in final edited form as:

Am J Phys Anthropol. 2017 November ; 164(3): 558–573. doi:10.1002/ajpa.23296.

Predictors of insubordinate aggression among captive female rhesus macaques

Shannon K. Seil, Darcy L. Hannibal^{*}, Brianne A. Beisner, and Brenda McCowan

Department of Population Health & Reproduction, School of Veterinary Medicine, UC Davis, Davis, CA 95616

California National Primate Research Center, UC Davis, Davis, CA 95616

Abstract

Objectives—Cercopithecine primates tend to have nepotistic hierarchies characterized by predictable, kinship-based dominance. Although aggression is typically directed down the hierarchy, insubordinate aggression does occur. Insubordination is important to understand because it can precipitate social upheaval and undermine group stability; however, the factors underlying it are not well understood. We test whether key social and demographic variables predict insubordination among captive female rhesus macaques.

Materials and Methods—To identify factors influencing insubordination, multivariate analyses of 10,821 dyadic conflicts among rhesus macaque females were conducted, using data from six captive groups. A segmented regression analysis was used to identify dyads with insubordination. Negative binomial regression analyses and an information theoretic approach were used to assess predictors of insubordination among dyads.

Results—In the best models, weight difference ($w = 1.0$; IRR = 0.930), age (dominant: $w=1.0$, IRR=0.681; subordinate: $w=1.0$, IRR=1.069), the subordinate's total number of allies ($w=0.727$, IRR=1.060) or non-kin allies ($w=0.273$, IRR=1.165), the interaction of the dominant's kin allies and weight difference ($w=0.938$, IRR=1.046), violation of youngest ascendancy ($w=1.0$; IRR=2.727), and the subordinate's maternal support ($w=1.0$; IRR=2.928), are important predictors of insubordination.

Discussion—These results show that both intrinsic and social factors influence insubordinate behavior. This adds to evidence of the importance of intrinsic factors and flexibility in a social structure thought to be rigid and predetermined by external factors. Further, because insubordination can precipitate social overthrow, determining predictors of insubordination will shed light on mechanisms underlying stability in nepotistic societies.

Keywords

dominance rank reversal; counter aggression; contra-hierarchical aggression; *Macaca mulatta*

^{*}Correspondence and current address: Darcy Hannibal, Department of Population Health & Reproduction, School of Veterinary Medicine, UC Davis, Davis, CA, 95616 USA, dlhannibal@ucdavis.edu, Phone: 530-752-1580, Fax: (530) 752-5845.

Dominance hierarchies are a common feature of social organization among gregarious mammals, serving to stabilize groups by mitigating intra-group conflict (Holekamp & Smale, 1991; Kaufmann, 1983; Kawai, 1958). While adherence to hierarchical structure is generally the norm in rank-based societies (e.g., dominant individuals direct aggression toward subordinates and limit their access to resources), there are exceptions and subordinates are occasionally aggressive toward dominants (Cooper & Bernstein, 2002; Isbell & Pruetz, 1998; Petit, Abegg, & Thierry, 1997). The benefits and costs of contra-hierarchical aggression, and thus the likelihood of its occurrence, are expected to vary primarily according to species dominance style (Isbell & Pruetz, 1998; Isbell & Young, 2002; Petit et al., 1997; Thierry, 1985). Species dominance styles vary along a continuum between egalitarian and despotic (de Waal & Luttrell, 1989; Isbell & Young, 2002; Sterck, Watts, & van Schaik, 1997; van Schaik, 1989). Among some primate taxa, particularly *Macaca*, despotism tends to covary with nepotism, a kin bias in relationships (Moore, 1992; Thierry, 1985; Wrangham, 1980). It is well documented that despotism and nepotism are associated with a greater frequency and severity of aggression that is more often directed down the hierarchy (Isbell & Young, 2002; Missakian, 1972; Silk, Samuels, & Rodman, 1981), as well as stricter hierarchies and low rates of contra-hierarchical aggression. However, individuals sometimes engage in contra-hierarchical aggression, and it is not well understood what leads them to take these risks. These events could be driven by social factors, such as the availability of conflict allies, or by intrinsic factors, such as body size. Contra-hierarchical aggression is of interest because: 1) it is a prerequisite and early marker of instability in dominance relationships, rank reversals, or social upheaval; 2) it is a way subordinate females may increase their social status and thus their fitness, and; 3) in despotic and nepotistic species it involves greater risk of severe retaliation by the dominant and her kin. We investigate the influence of age, body weight, and conflict allies on the likelihood of insubordinate aggression among rhesus macaque females, which are well documented as both nepotistic and despotic.

Insubordination

Many studies have investigated individual-level variance in dominance relationships, most using rank outcomes (e.g. rank reversal, deviation from genealogically expected rank) as indices of variation in dominance (Chapais, 1992; Datta, 1983; Lea, Learn, Theus, Altmann, & Alberts, 2014). This approach, while straightforward, is limited because: 1) rank reversals and unexpected rank outcomes are relatively uncommon, especially in despotic species, and; 2) it does not account for variation in the degree to which one animal is dominant to another, even though such subtle variation in degree of dominance might influence conflict dynamics (McCowan et al., 2011), overall health (Beisner, Vandeleest, Hsieh, Fujii, & McCowan, 2014), resource holding potential, and the likelihood of rank reversal. We propose insubordinate aggression as a more common and sensitive behavioral index of dyadic power dynamics that may allow a more nuanced understanding of variance in dominance relationships.

Contra-hierarchical aggression can be observed when a dominance relationship is unsettled or ambiguous, but can also occur among dyads with determinate dominance relationships. We use the term insubordination to refer only to those instances of contra-hierarchical

aggression that occur in determinate dominance relationships. Because insubordination can result in rank reversals and deviations, the results of studies relating to rank outcomes are pertinent to insubordination and are discussed below.

Intrinsic versus extrinsic factors in dominance outcomes

Previous work has shown that in despotic-type societies, bidirectional aggression and rank reversals are infrequent and more often result in serious injury (Missakian, 1972; Silk et al., 1981) relative to less despotic and more egalitarian societies (Isbell & Pruettz, 1998; Isbell & Young, 2002). When a society is also nepotistic (e.g. vervets, macaques, baboons, some capuchins), dominance rank is inherited by virtue of alliances with close kin and consistent patterns of kin support (Bernstein & Williams, 1983; Chapais, 1992; Datta, 1988; Kawai, 1958; Silk et al., 1981). Patterns of maternal support create a system of ‘youngest ascendancy’, in which sisters rank according to inverse birth order (Chapais & Schulman, 1980; Datta, 1988; Horrocks & Hunte, 1983), and kin commonly form agonistic alliances against non-kin, resulting in ‘matrilines’ that occupy distinct rank tiers within the group (Berman, 1980; Chapais, 1988; Datta, 1988; but see Fushing, McAssey, Beisner, & McCowan, 2011). Such hierarchies tend to be highly predictable and stable over time, and individuals’ intrinsic competitive ability (e.g. age, body size) appears much less influential than extrinsic factors, such as social alliances, in determining dominance relationships (Missakian, 1972; Sade, 1967). However, deviations from expected rank order in despotic and nepotistic primate societies have been documented. For example, among macaques, multiple matrilines may occupy the same rank tier, and some females may occupy a rank separate from the rest of their kin (Bernstein, 1969; Chikazawa, Gordon, Bean, & Bernstein, 1979; Datta & Beauchamp, 1991; Fushing et al., 2011). Although social support (e.g. kin and non-kin conflict allies) is associated with these deviations (Chapais, 1988; Datta & Beauchamp, 1991) the influence of intrinsic factors such as age and weight needs further investigation, as explained below.

Age and weight

Among mammal species characterized by individualistic hierarchies, such as elephants, red deer, and mantled howler monkeys, intrinsic competitive ability is the primary determinant of dominance rank (e.g. Archie, Morrison, Foley, Moss, & Alberts, 2006; Clutton-Brock & Guinness, 1982; Jones, 1980). While intrinsic attributes can be influential in nepotistic societies, the extent and nature of this influence is unclear. There is much evidence supporting that age and weight influence rank acquisition and maintenance in primate males, who tend to emigrate from kin at sexual maturity (Bissonnette, de Vries, & van Schaik, 2009; Raleigh, McGuire, Brammer, Pollack, & Yuwiler, 1991; Sapolsky & Share, 1994; Sebastian, 2015; Sprague, 1998). There is some limited evidence that intrinsic factors may have a role in adult macaque female hierarchies (Sebastian, 2015). However, for nepotistic female primates, the influence of age and weight on dominance is most striking during maturation. Juvenile females undergo a period of rank acquisition during which they are initially unable to dominate their mother’s subordinates in her absence, but as they mature they eventually acquire dominance over all females subordinate to their mother (Bernstein & Williams, 1983; Datta, 1983; de Waal & Luttrell, 1985; Sade, 1967). While maturation

affects the rate and timing of dominance acquisition, it generally does not appear to impact females' positions in the hierarchy as adults. Females acquire their genealogically expected rank (i.e. the rank just beneath their mother and above older siblings) at around the age of sexual maturation: three for vervets (Lee, 1983), four for macaques (Bernstein & Williams, 1983; Datta, 1983; Sade, 1967; Wilson, Gordon, Blank, & Collins, 1984), and five for savanna baboons (Johnson, 1987; Lee & Oliver, 1979). Thereafter, mature females enter a period of "rank maintenance" wherein their relative rank in the group changes very little (Chapais, 1992). However, geriatric females can undergo rank reversals and become outranked by their adult daughters (Chikazawa et al., 1979; Combes & Altmann, 2001; Silk et al., 1981). Additionally, young females whose mothers die before they mature may never attain their genealogical expected rank or have difficulty maintaining their current rank (Datta, 1988; Missakian, 1972).

Although it is clear that age and weight influence the acquisition and, to some extent, maintenance of dominance in nepotistic species, it is unknown whether the body weight of adult females in their prime influences either deviant rank outcomes or the likelihood of engaging in or receiving insubordination. While social relationships can be observed in wild populations, intrinsic competitive abilities of group members are difficult to quantify in wild populations. Therefore, the lack of evidence for intrinsic size, strength or competitive ability, may be an artifact of what is most feasible to test in study populations. Captive populations provide an opportunity to record exact birth year and body mass of each group member. Since rank reversals require insubordination, we hypothesize that factors influencing rank acquisition and maintenance might also influence insubordination. We therefore predict that body weight and age have the potential to influence the likelihood of insubordination, even when compared to extrinsic factors. Specifically, we predict that: 1) high weight disparity reduces the likelihood of insubordination if the dominant outweighs the subordinate, or promotes it if the subordinate outweighs the dominant, and; 2) young adult females are more likely to receive insubordinate aggression and less likely to initiate it than older females.

Social factors

Social support influences dominance rank in nepotistic species, primarily through agonistic aid in conflicts (Bernstein & Ehardt, 1985; Chapais, 1988; Datta, 1988). Kin represent a key source of agonistic support for females in nepotistic societies and certain aspects of kin support are known to influence rank acquisition and maintenance, such as the presence of a female's mother or other close maternal kin, and these may also influence contra-hierarchical aggression (Bernstein, 1969; Chapais, 1988; Engh, Hoffmeier, Seyfarth, & Cheney, 2009; Langergraber, 2012). For example, when mothers die before their youngest surviving daughter reaches maturity, violations of the "youngest ascendancy rule" (described above) are more likely (Datta, 1988; Missakian, 1972).

Although kin are more likely to provide agonistic aid in conflicts than non-kin, non-kin also intervene in conflicts, and studies have demonstrated that agonistic aid from non-kin can influence dominance rank (Chapais, 1992). Chapais (1988) suggested that non-kin alliances are critical to hierarchical stability. Chapais reasons that if each matriline were to separately compete for dominance, then random demographic shifts in the relative size and strength of

matrilines would likely shift power away from dominant matriline, allowing destabilizing matriline rank reversal (i.e. social overthrow). Therefore, non-kin are expected to form alliances against females ranking beneath them, thus making the hierarchy robust against inevitable changes in the relative strength and size of individual matriline. This hypothesis has been supported by evidence that females typically support the dominant opponent in conflicts and intervene on fights when they outrank the target, which results in collective suppression of low ranking animals (Chapais, 1983; Chapais, Girard, & Primi, 1991; Hunte & Horrocks, 1987; Netto & Van Hooff, 1986).

Taken together, this evidence highlights the importance of both non-kin and kin allies in the maintenance of rank and stabilization of hierarchies. Since a female's mother is the ally most critical to her rank acquisition and maintenance, we predict that the presence of an adult female's mother in the group will make her more likely to initiate insubordination and less likely to receive it. Likewise, we predict that females with many kin and non-kin allies will be more likely to initiate insubordination, and less likely to receive it. We further expect that social factors may modulate intrinsic factors and thus there may be interaction effects between them.

MATERIALS AND METHODS

Study site and groups

This study was conducted at the California National Primate Research Center (CNPRC), in Davis, California, from June 2008 to April 2010. For analyses of insubordination behavior among adult females, the study subjects were 357 adult female rhesus macaques ranging in age from 4–25 years of age (yoa). In addition, the above subjects plus 130 three-year-old females and 247 males three years of age and older were included in dominance rank and probability analyses. We also tallied each female's number of conflict allies (defined in Table 3). Three-year-olds were excluded from insubordination data because females do not typically attain adult rank until about four years of age (Bernstein & Williams, 1983; Datta, 1983; Sade, 1967). Rhesus macaque females typically reach sexual maturity between the ages of three and four (Wilson et al., 1984); therefore, four-year-old females are likely to have attained both adult dominance and sexual maturity. No data were collected on juveniles.

The subjects were members of six mixed-sex and age social groups (groups 1, 5, 8, 10, and 18) housed separately in 0.2 ha corrals. Corrals contain some perching and climbing structures, but they do not impede visibility and both the subjects and observers have line of sight and easy access to view all areas, which allowed observers to record social interactions from beginning to end. The groups were each comprised of between 108–197 individuals. Each group was observed for six hours per day, four days per week, for 10 weeks distributed across the entire study period, with an average of 193 hours of observation per group (Table 1). Data were collected by four observers and inter-observer reliabilities had a mean 91% agreement across all recorded behaviors with a standard deviation of 3%; range: 86–94%, across three observers. All groups had been well-established breeding groups for at least 10 years each, with multi-generational matrilineal social structure.

Two observers at a time cooperatively recorded most or all aggressive, submissive, and status interactions among male and female group members three years of age and older using an event-sampling design that preserved the temporal sequence of long bouts of conflict (Beisner et al., 2011). Observers each focused on one half of the corral area; when subjects passed through both areas during the course of one fight, observers compared records to consolidate their observations into a single recorded event. These events were characterized as an ordered series of dyadic transactions, initiated by one individual and directed toward a recipient, whose response or lack of response was recorded. Prolonged or polyadic interactions were recorded as a series of dyadic interactions, with no limit on the number of transactions occurring in a single event. For interactions involving multiple initiators or recipients, dyadic transactions were tagged to indicate co-aggression or joint receipt of aggression.

Data analysis

Dominance probability—Unidirectional dyadic aggressive interactions among all adults (3 yoa, both sexes), wherein the initiator was aggressive and the recipient submissive, with no aggression directed toward the initiator and no third party support (i.e. interventions), were analyzed to generate dominance rank and probability (DP) scores using the method described in Fushing et al. (2011). The DP method produces a probability that one animal will “win” a fight against another, and although this analysis excludes non-aggressive status signals, such as bared teeth displays, previous work shows that DP predicts the status signaling network (Beisner, Hannibal, Finn, Fushing, & McCowan, 2016) and this same trend is true in the data presented here. The DP analysis is a social network approach that incorporates direct and indirect network pathways between each pair of individuals to supplement direct observations of aggressive interactions, filling in missing cells of the win/loss matrix with the information from the indirect aggression network pathways (Fushing et al., 2011). Thus, even if two animals are never observed to interact, strong predictions about their dominance relationship can be made provided they have numerous and consistent indirect connections through other group members. The resulting matrix of subjects’ dyadic DP scores is a summary of all direct and indirect aggression pathways for that dyad and has a possible range from 0.0 to 1.0, with 0.0 indicating animal A has entirely certain subordination to animal B, 0.5 indicating an entirely ambiguous relationship between a dyad, and 1.0 indicating animal A has entirely settled and determinate dominance over animal B. DP scores were used for two purposes in this study: 1) to provide information about the direction and certainty of dyadic dominance relationships, and 2) to generate a linear hierarchy for all adult females in each group using a matrix approach.

Identifying determinate versus ambiguous dominance relationships and detecting true insubordination—Within a hierarchy, all dyads with discernable dominance (i.e. unequal wins/losses) are typically assumed to have determinate dominance relationships (de Vries, 1998). In reality, however, some dyads have ambiguous or changing dominance relationships (Albers & de Vries, 2001; Fushing et al., 2011), where more frequent bidirectional aggression is expected. Since contra-hierarchical aggression is not truly insubordinate if the relationship is ambiguous or unsettled, and these dyads would add considerable noise to analyses of insubordination, we sought to establish whether dyads in

our study groups had an identifiable breakpoint between determinate versus ambiguous dominance relationships. If so, it would be important to exclude ambiguous ones. Although there is likely a continuum between determinate versus ambiguous dominance and a strict categorization will have some amount of error, the purpose here is not to make an exact distinction, but rather to determine whether a distinction is reasonable to limit the noise that ambiguous relationships would introduce into analyses of insubordination.

We analyzed DP scores and bidirectional aggression data to examine potential distinctions between ambiguous and determinate dominance dyads. First, dyads with DP scores ≤ 0.5 (i.e., the lower triangle of the matrix) were dropped from the analysis so that (a) each dyad was represented only once in the data and (b) dyads with perfectly ambiguous relationships due to a lack of any direct or indirect dominance interactions (DP = 0.5) were omitted (Fig. 1, see step 1, processes b and c). We then examined the remaining dyads with DP scores >0.5 (13,298 aggressive interactions among 5,810 adult female dyads, with 1,360 contra-hierarchical interactions from 1,045 dyads), to identify a DP threshold between ambiguous and determinate relationships.

To do this we used bidirectional dyadic aggression data, defined as when both opponents exhibited aggression, regardless of which animal won the encounter. This is distinct from the unidirectional aggression data used to calculate dominance probability, wherein only the initiator exhibited aggression. We then calculated the per-dyad rate of bidirectional aggression (count of bidirectional aggression divided by total conflicts for each dyad) and the average rate of bidirectional aggression among dyads of each dominance probability centile. We then regressed bidirectional aggression rate on dominance probability centile, using the “segmented” package in R (v. 3.1.2) to identify the optimal number and location of breakpoints in the slope of the relationship (Fig. 1, see step 2, processes d and e) (Muggeo, 2008; R Core Team, 2013). The segmented regression of bidirectional aggression against DP probability centiles resulted in two segments (Fig. 2). The best breakpoint in the linear relationship, identified using maximum likelihood, was DP = 0.745 (SE=0.0319, 95% CI= 0.681–0.809). The segment from DP=0.52 to 0.745 had a slope of -0.469 and the segment from 0.745 to 1 had a slope of 0.063. We used this breakpoint of DP = 0.745 as a threshold for categorization of ambiguous versus determinate dominance dyads, and used it as a cut-off for analyses of insubordinate aggression. All dyads with a dominance probability below this breakpoint were dropped, with 10,821 aggression records involving 3,790 dyads remaining for further analyses; 563 of dyads analyzed showed insubordination.

Potential confounds and subpopulation differences—Age and weight are potentially collinear for sexually mature young adult rhesus macaque females who have not yet attained full adult body size (Campbell & Gerald, 2004). Age and weight were indeed correlated for our young adult female (4–7 yoa) ($r=0.54$, $P<0.001$), but not full adult female (>7 yoa) ($r=0.008$, $P=0.91$) subjects. Another potential issue is subpopulation differences in insubordination dynamics for kin versus non-kin dyads. Insubordination is potentially predicted by different variables for kin versus non-kin (such as youngest ascendancy violation, which is only relevant to kin dyads).

One potential statistical method for dealing with both of these issues is to introduce interactions terms. However, if one variate is not relevant (e.g., youngest ascendancy violation, or weight for young adults), then including it in the model unnecessarily adds to the complexity of modeling that portion of the sample, depletes degrees of freedom, and reduces the quality of statistical modeling. This reduction in model quality is particularly undesirable for the information theoretic approach. Another option is to create subsets by key population demographic categories to arrive at the best model set for each subpopulation, which requires a large enough total sample that each subset still has sufficient power. The total sample size for this study is sufficiently large to generate subsets for each subpopulation to produce best model sets appropriate for an information theoretic approach, with the smallest subset containing 210 dyads. Based on the criteria for age and relatedness described above and the large sample size, separate analyses were conducted for the following subsets of dyads: 1) both the dominant and subordinate are full adults (N=998); 2) the dominant is any adult age, but the subordinate is a young adult (N=1859); 3) the dominant is a young adult, but the subordinate is any adult age (N=1586), and; 4) the dominant and subordinate have a kin relationship and are both any adult age (N=210). Weight and age were only jointly modeled in the older age category in which they were not correlated; for dyads including at least one young animal, the effect of weight was not modeled. Weight was not examined in the kin dyad subset because it included both young and full adult females and was not large enough to further subset.

Insubordinate aggression analyses—Counts of insubordinate events per dyad were fit using Stata (version 14.0) to mixed-effects negative binomial regression models for each data subset defined above using a distribution, with total number of aggressive interactions observed for the dyad as an exposure variable (Rabe-Hesketh & Skrondal, 2012). The count of events per dyad range from 0 to 10, with a mean of 0.23; thus, insubordination events occur infrequently, as expected for despotic and nepotistic rhesus macaque females. A random effect was included for group (N=6). A variety of fixed effects and interactions were tested in the models, as described in Table 2, which included variables specific to the hypotheses being tested as well as dominance rank variables since they are expected to be important for models of insubordination. For each variate used to test the hypotheses, we report the incidence rate ratio (IRR) calculated from the regression coefficients. The IRR for variates in our models is the estimated factor by which the number of insubordination events will increase (IRR > 1) or decrease (IRR < 1) for a one unit increase in the variate, given that all other variates in the model are held constant over approximately 193 hours of observation (amount of time study groups were observed).

An information theoretic (IT) approach was used to assess models using goodness-of-fit measures, Akaike Information Criterion differences (ΔAIC) in scores, model weights, and variate weights to determine the best set of models and the variates that best explain insubordination (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011). Variables and interactions that were retained in the best model sets are summarized in Table 3. All models were considered (up to a limit reasonable for our sample size) that had both a model chi-square and an AIC score less than the random effects only model, which indicates a model is minimally good and better than the random effects only model (all models tests

are available in the supplementary tables) (Anderson & Burnham, 2002). Models with a chi-square and AIC worse than an empty model (the random effects only model) are essentially worse than a model with no explanatory value and thus not worth considering (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011). Models that violated the principal of parsimony (not an improvement over a simpler model) were eliminated from the best model set (Burnham & Anderson, 2002; Richards, 2005). Then a candidate set of models with a $\Delta AIC < 10.0$ was selected to calculate model likelihoods, Akaike weights, and evidence ratios to determine the strength of the evidence for these models (Burnham & Anderson, 2002; Burnham et al., 2011; Grueber et al., 2011; Richards, 2005; Symonds & Moussalli, 2011). Continuing with the IT method, a best model set was determined based on an evidence ratio of ≥ 10 , which generally includes only models with $\Delta AIC < 5$, and weights were then renormalized (Burnham & Anderson, 2001, 2002). From this final best model set, variate weights (w) were calculated by summing the model weights across all models that contained the variate (Burnham and Anderson 2002). For variates of interest, marginal effects (margins command) and plots (plot command) were produced from the best-fit models (Hardin & Hilbe, 2007; Rabe-Hesketh & Skrondal, 2012).

RESULTS

How do age and weight affect insubordinate aggression?

Age—For the subset of dyads wherein both the dominant and subordinate opponent were full adult females (>7 yoa), the set of best-fit models included an interaction between the dominant's age and the subordinate's age ($w = 0.766$, best-fit model IRR = 0.990; SE ± 0.004) (Tables 4 and 5), with the greatest increase in insubordinate events when there is a dyad combination of an eight-year-old dominant and a 22-year-old subordinate, moderately high when the dominant is 20 years of age or older and the subordinate is 8–12 years of age, and the lowest when both opponents are 20 years of age or older (Fig. 3). For the subset of dyads wherein the dominant opponent was a young adult (4–7 yoa), the set of best-fit models included the ages of the dominant ($w = 1.0$, best-fit model IRR = 0.681; SE ± 0.039) and the subordinate ($w = 1.0$, best-fit model IRR = 1.069; SE ± 0.013), but no interaction of dominant and subordinate age (Tables 4 and 5). When considering the age of a young adult dominant, the greatest number of events are predicted when the dominant is four years of age, with a steep decline through age seven (Fig. 4A). For the subordinate opponent of a young adult dominant, the predicted number of events increase steeply from a low at age four through a high at age 20 (Fig. 4B). Similarly, for the subset of dyads wherein the subordinate opponent was a young adult, the set of best-fit models included the ages of the dominant ($w = 1.0$, best-fit model IRR = 0.936; SE ± 0.016) and the subordinate ($w = 1.0$, best-fit model IRR = 1.200; SE ± 0.083), with young dominants receiving more insubordination and older subordinates initiating more insubordination, but the predicted mean insubordination events remains below 0.2 for all age combinations in this subset.

Weight—Weight difference (dominant body weight – subordinate body weight, kg) was tested only for the subset of dyads wherein both opponents were full adults (>7 yoa). Weight difference in this subset ranged from -6.75 to 7.6 kg and was included in all four of the best-fit models for this age category, but in the top three of the four models it appeared in

interaction with the dominant's number of kin allies (see kin allies section below). In model 4, high weight disparity ($w = 0.062$; IRR = 0.930; SE ± 0.030) (Tables 4 and 5) predicted marginal means for insubordination events are highest when the subordinate outweighs the dominant by -7 kg and lowest when the dominant outweighs the subordinate by 7 kg.

How do the number of kin and non-kin allies and the presence of a mother affect insubordinate aggression?

For the subset of dyads wherein both the dominant and subordinate opponent were full adults (>7 yoa), the set of best-fit models included an interaction between dyadic weight difference and the dominant's count of kin allies ($w = 0.925$, best-fit model IRR=1.046; SE ± 0.018) and the subordinate's total allies (kin + non-kin allies) ($w = 1.0$, best-fit model IRR=1.091; SE ± 0.021) (Tables 4 and 5), with kin allies reducing insubordination received for a dominant and total allies increasing insubordination initiated by a subordinate. A dominant female at the most extreme weight disparity (nearly -7 kg) has the greatest risk of receiving insubordination (predicted mean events = 1.1) if she has no kin allies. However, her risk drops dramatically (although still rather high for a rhesus macaque female) with only two kin allies (predicted mean events = 0.52), and is negligible with six or more kin allies (predicted mean events < 0.15) (Fig. 5).

For non-kin dyads wherein the dominant was a young adult, the set of best-fit models included effects for the presence of the dominant's mother ($w = 0.795$; IRR=0.758; SE ± 0.10), but variables for the dominant's allies were not retained in any of the best-fit models. However, for this subset, the subordinate's count of non-kin allies ($w = 0.273$, best-fit model IRR=1.065; SE ± 0.023) or the subordinate's total allies (kin + non-kin allies) ($w = 0.727$, best-fit model IRR=1.060; SE ± 0.019) (Tables 4 and 5) (Fig. 6) were in the best-fit models. For non-kin dyads wherein the subordinate was a young adult, the set of best-fit models included effects for the presence of the subordinate's mother ($w = 0.209$; IRR=1.472; SE ± 0.280), and either the subordinate's count of non-kin allies ($w = 0.172$, best-fit model IRR= 1.081; SE ± 0.034) or the subordinate's total allies (kin + non-kin allies) ($w = 0.828$, best-fit model IRR=1.081; SE ± 0.029), which are all associated with an increase in insubordination (Tables 4 and 5).

Among kin dyads, the presence of the subordinate's mother ($w = 1.0$; best-fit model IRR=2.928; SE ± 1.248) (Fig. 7), as well as the subordinate's count of non-kin allies ($w = 0.757$, best model IRR=1.160; SE ± 0.083) appear in the best model set (Tables 4 and 6), both of which increase insubordination. Additionally, violation of the youngest ascendancy rule is in all the kin dyad best models ($w = 1.0$; best-fit model IRR=2.727; SE ± 1.002) (Fig. 8) (Tables 4 and 6), and thus is an important predictor of increased insubordinate aggression.

DISCUSSION

Our results show that the nature and stability of dyadic dominance relationships vary according to a suite of intrinsic and extrinsic characteristics. Even within well-established dominance relationships congruent with genealogical expectation, there is predictable variability in the degree of deference offered to dominants. Specifically, our results show

that both intrinsic (weight, age) and extrinsic (social support) attributes influence individuals' likelihood of engaging in or receiving insubordinate aggression. We find that kinship modulates the influence of conflict allies on insubordination—having many non-kin allies increases the likelihood of initiating insubordinate aggression, whereas kin allies appear to be more important for protecting against insubordination. Further, we find that social support modulates the influence of disparity in size/strength. Our results highlight the important influence of social support and position as well as body size on exertion of power within dominance relationships, and by extension on variance in attainment and retention of expected rank. This adds to growing evidence that dominance relationships in nepotistic species are more complex, and less predictable, than previously assumed.

Age

Age disparity influenced initiation and receipt of insubordination. When the dominant was older than the subordinate, insubordination was less likely, but when the subordinate was older than the dominant, the likelihood of insubordination increased. This effect was present in all three age groups modeled, even in the mature age group for which increasing age was not positively correlated with size/strength. This suggests that age has an effect on dominance acquisition and maintenance independent of associated physical competitive ability. This effect could be associated with potential correlates of age including experience and expanded social networks, or it could reflect residual effects of size disparity during development; i.e., juveniles are at a physical disadvantage to older animals, and power imbalances established during this period may persist into adulthood despite the disappearance of any physical inequality. Theory predicts and empirical evidence suggests that advanced age is associated with decline in both cognitive and physical competitive ability (Borries, Sommer, & Srivastava, 1991; Hrdy & Hrdy, 1976; Van Noordwijk & Van Schaik, 1987). Our results do show evidence of an effect of geriatric decline on insubordination rates; females 20 years of age and older are increasingly likely to receive insubordination from younger females. However, the number of geriatric females is relatively small compared to other ages in that subset.

Weight

We find that body weight disparity influences insubordination rates; when the dominant is heavier, insubordination is less likely, and when the subordinate is heavier, insubordination is more likely. This suggests that subordinate females assess their own size/strength relative to their opponent and that this information is used to gauge their level of tolerance or deference. Further, we find that social support, in particular the dominant female's kin support, modulates the influence of weight disparity. Although insubordination is more likely when the subordinate outweighs the dominant, a weaker dominant's kin allies may protect her from insubordination. Indeed, with few or no kin allies in conflicts, a dominant female at a weight disadvantage of -6kg has the highest risk of insubordination over any other metrics considered in any of the models.

Body size fundamentally underlies dominance in many animal species (Parker, 1974). However, in nepotistic species, rank and power are thought to be primarily determined through inheritance and kin support rather than through physical contests (Hrdy & Hrdy,

1976; Sade, 1967; Missakian, 1972). Studies have demonstrated that for several nepotistic species, high-ranking animals are larger than low-ranking animals (Small, 1981; Sprague, 1998), and eat more and better quality food with less effort (Van Noordwijk & Van Schaik, 1987). Given this evidence, and if dominance is indeed strictly heritable, then it follows that dominance causes weight gain and not vice versa. Another non-mutually exclusive possibility is that body size may directly influence attainment and maintenance of dominance. Several lines of evidence support this, such as the correlation between attainment of physical maturity and ability to defend rank independent of maternal support (Kawai, 1958; Lea et al., 2014). However, no studies have empirically evaluated whether body size directly affects dominance in nepotistic female primates. Our results suggest that weight likely influences ability to acquire and maintain rank. This points to the possibility that weight gain is both a cause and an effect of high rank; if so, rank-associated weight gain could function to reinforce and stabilize existing dominance hierarchies. Importantly, however, kin allies appear to be able to compensate for a dominant female's physical weakness. We discuss this further below.

Kin allies and maternal support

Agonistic aid from a juvenile female's mother, and to a lesser extent her siblings, is thought to be the primary mechanism by which a female acquires her genealogically expected dominance rank (Bernstein & Williams, 1983; Datta & Beauchamp, 1991; Engh et al., 2009). Without kin support, females are less likely to attain expected rank (Datta, 1988; Lea et al., 2014) and more vulnerable to rank reversal (Chapais, 1988; Lea et al., 2014). Accordingly, we find that the presence of mothers is influential for both initiating and receiving insubordination, particularly for young adult females. Further, having many kin allies appears to protect dominant females against receipt of insubordination, at least among fully mature adult females. The importance of kin in protecting against insubordination is especially pronounced when a dominant female is physically weaker than her subordinate opponent. Conversely, availability of agonistic support from kin does not appear to embolden subordinate females to initiate insubordination. Furthermore, kin support beyond that provided by a mother does not appear to strongly influence insubordination among young females. The lack of detectable effects of kin allies on initiation of insubordination, and on both initiation and receipt of insubordination among young females, is surprising because kin support is the fundamental driver of social structuring in nepotistic societies, and is a critical determinant of rank and status. Dominant matriline are occasionally challenged and defeated by revolutionary coalitions, which are typically comprised of entire matriline or groups of allied matriline (Ehardt & Bernstein, 1986; Oates-O'Brien, Farver, Anderson-Vicino, McCowan, & Lerche, 2010). In such cases kin alliances are the key factor that allows lower ranking animals to outrank higher ranking animals. Our results provide support for the importance of kin allies for rank maintenance in some circumstances, but no support for the importance of kin coalitions in challenging dominants.

Our results should not be taken to indicate that kin support is not important for rank reversals and social overthrows; many studies and documented cases have demonstrated that coalitions of kin can and do instigate coordinated revolutions (Ehardt & Bernstein, 1986; Oates-O'Brien et al., 2010). We find that subordinate females are not emboldened to engage

in insubordination by having many kin allies, perhaps because kin allies are not likely to intervene against higher ranking animals, and/or because agonistic aid from kin allies would not improve the subordinate's situation under most circumstances. Perhaps insubordinate interventions by kin are sufficiently provocative that the associated risk of conflict escalation and severe retaliation outweighs the benefits of such behavior in the majority of cases.

Non-kin allies

The effect of non-kin allies on insubordination was pronounced, but specific to the initiation of insubordination only, and not receipt of insubordination. The number of non-kin allies a female had was one of the most consistent predictors of her likelihood of initiating insubordination in all model sets, for both kin and non-kin opponents. Contrary to our prediction, non-kin allies did not influence dominant females' receipt of insubordination. Theory predicts and studies demonstrate that non-kin allies are critical to maintenance of dominance and hierarchical stability. In theory, non-kin should form alliances against lower-ranking females, in order to prevent revolutionary coalitions that could otherwise threaten the status of either ally's matriline (Chapais, 1988, 1992). Studies have shown that when females intervene in the conflicts of non-kin, they preferentially support the dominant opponent, and intervene most often in non-kin conflicts when they outrank the target (Chapais, 1983; Chapais et al., 1991; de Waal & Luttrell, 1988; Hunte & Horrocks, 1987; Netto & Van Hooff, 1986). However, females do occasionally intervene against the dominant opponent, even if the target outranks them. Males are more likely than females to intervene impartially or against the dominant opponent; such male 'policing' is thought to mitigate intra-group conflict and promote group stability (Beisner & McCowan, 2013; Flack, Girvan, de Waal, & Krakauer, 2006). Interventions influence conflict outcomes (Beisner & McCowan, 2013; Ehardt & Bernstein, 1992). Furthermore, cercopithecine primates are aware of the alliances of others, and alter their behavior accordingly (Cheney & Seyfarth, 1999). These studies collectively suggest that interventions by non-kin should be influential for both rank maintenance and rank reversal. We therefore predicted that having more non-kin conflict allies should reduce a dominant female's likelihood of being challenged by subordinates because potential challengers might anticipate the involvement of these allies. Likewise, we predicted that having many non-kin allies would increase a subordinate's likelihood of initiating a challenge, because she could appeal to these allies for support. Our results support the latter prediction that non-kin allies influence a subordinate's likelihood of initiating insubordinate aggression, but fail to support the prediction that non-kin allies can help a dominant female maintain rank through inhibiting insubordination.

CONCLUSION

The results of this study suggest that there is considerable variation in the circumstances under which subordinate females behave aggressively toward dominants in a nepotistic society, and that insubordination can occur even when dominance is relatively certain. Dominance relationships in nepotistic societies are indeed dependent on genetic relatedness and kin support, but also on support from non-kin and intrinsic competitive ability. In particular, we find that body size disparities influence dominance outcomes, and that kin conflict allies mitigate the effects of size disparities for rank maintenance while non-kin

allies are more influential in emboldening subordinate females to challenge dominants. Overall, our results highlight that, despite a rigid and despotic social environment, rhesus macaque females do not passively accept their inherited social status, but rather are dynamic agents who appear to consistently monitor and test the relationships that limit their fitness, and integrate complex information to determine whether to defer to or rebel against the impositions of dominant group members. Our research sheds light on the continuum between total dominance and total equality. Where a particular dyad falls on this continuum—as reflected by the occurrence of insubordinate aggression—depends in part on their relative attributes, both intrinsic and social.

Acknowledgments

The project was supported by NIH grant R24 RR024396, PR51 RR000169 and approved by the UC Davis IACUC. We would like to thank Allison Heagerty, Megan Jackson, Ashley Cameron, and Ashleigh Day for their assistance in the logistical and conceptual development of this study and additional thanks to Megan Jackson for assisting with data collection. SS, DH, and BB developed the research questions, hypotheses, and analytical methods; SS analyzed the data. BM designed the study and data collection, as well as provided the materials; BB and SS performed the data collection; SS, DH, BB, and BM wrote and revised the manuscript. We would also like to thank our editors and reviewers for their helpful suggestions, which ultimately improved the manuscript.

LITERATURE CITED

- Albers PCH, de Vries H. Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*. 2001; 61:489–495. DOI: 10.1006/anbe.2000.1571
- Anderson DR, Burnham KP. Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management*. 2002:912–918.
- Archie EA, Morrison TA, Foley CA, Moss CJ, Alberts SC. Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*. 2006; 71(1):117–127.
- Beisner, B., Vandeleeuw, J., Hsieh, F., Fujii, K., McCowan, B. Mean dominance relationship certainty is better than rank at predicting diarrhea incidence and wounding in captive rhesus macaques (*Macaca mulatta*). Paper presented at the annual meeting of the American Society of Primatologists; Decatur, GA: 2014 Sep.
- Beisner BA, Hannibal DL, Finn KR, Fushing H, McCowan B. Social power, conflict policing, and the role of subordination signals in rhesus macaque society. *American Journal of Physical Anthropology*. 2016; 160(1):102–112. DOI: 10.1002/ajpa.22945 [PubMed: 26801956]
- Beisner BA, McCowan B. Policing in nonhuman primates: Partial interventions serve a prosocial conflict management function in rhesus macaques. *PLoS ONE*. 2013; 8(10):e77369. [PubMed: 24167570]
- Berman CM. Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. *International Journal of Primatology*. 1980; 1(2):153–170.
- Bernstein IS. Stability of the status hierarchy in a pigtail monkey group (*Macaca nemestrina*). *Animal Behaviour*. 1969; 17:452–458.
- Bernstein IS, Ehardt CL. Agonistic aiding: kinship, rank, age, and sex influences. *American Journal of Primatology*. 1985; 8(1):37–52.
- Bernstein IS, Williams LE. Ontogenetic changes and the stability of rhesus monkey dominance relationships. *Behavioural Processes*. 1983; 8(4):379–392. [PubMed: 24897682]
- Bissonnette A, de Vries H, van Schaik CP. Coalitions in male Barbary macaques, *Macaca sylvanus*: strength, success and rules of thumb. *Animal Behaviour*. 2009; 78(2):329–335.
- Borries C, Sommer V, Srivastava A. Dominance, age, and reproductive success in free-ranging female Hanuman langurs (*Presbytis entellus*). *International Journal of Primatology*. 1991; 12(3):231–257.
- Burnham KP, Anderson DR. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*. 2001; 28(2):111–119. doi: <http://dx.doi.org/10.1071/WR99107>.

- Burnham, KP., Anderson, DR. Model selection and multimodel inference: A practical information-theoretic approach. 2. New York: Springer; 2002.
- Burnham KP, Anderson DR, Huyvaert KP. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*. 2011; 65(1):23–35.
- Campbell BC, Gerald MS. Body composition, age and fertility among free-ranging female rhesus macaques (*Macaca mulatta*). *Journal of Medical Primatology*. 2004; 33(2):70–77. DOI: 10.1111/j.1600-0684.2004.00055.x [PubMed: 15061719]
- Chapais, B. Dominance, relatedness and the structure of female relationships in rhesus monkeys. In: Hinde, RA., Berman, CM., editors. *Primate social relationships: An integrated approach*. Oxford: Blackwell; 1983. p. 208-217.
- Chapais B. Rank maintenance in female Japanese macaques: experimental evidence for social dependency. *Behaviour*. 1988:41–59.
- Chapais, B. The role of alliances in social inheritance of rank among female primates. In: Harcourt, AH., de Waal, FB., editors. *Coalitions and alliances in humans and other animals*. Oxford: Oxford University Press; 1992. p. 29-60.
- Chapais B, Girard M, Primi G. Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. *Animal Behaviour*. 1991; 41(3):481–491.
- Chapais B, Schulman SR. An evolutionary model of female dominance relations in primates. *Journal of Theoretical Biology*. 1980; 82(1):47–89. [PubMed: 6772881]
- Cheney DL, Seyfarth RM. Recognition of other individuals' social relationships by female baboons. *Animal Behaviour*. 1999; 58(1):67–75. [PubMed: 10413542]
- Chikazawa D, Gordon TP, Bean CA, Bernstein IS. Mother-daughter dominance reversals in rhesus monkeys (*Macaca mulatta*). *Primates*. 1979; 20(2):301–305.
- Clutton-Brock, TH., Guinness, FE. *Red deer: behavior and ecology of two sexes*. Chicago, IL: University of Chicago press; 1982.
- Combes SL, Altmann J. Status change during adulthood: life-history by-product or kin selection based on reproductive value? *Proceedings of the Royal Society of London B: Biological Sciences*. 2001; 268(1474):1367–1373.
- Cooper MA, Bernstein IS. Counter aggression and reconciliation in Assamese macaques (*Macaca assamensis*). *American Journal of Primatology*. 2002; 56(4):215–230. DOI: 10.1002/ajp.1076 [PubMed: 11948638]
- Datta, SB. Relative power and the acquisition of rank. In: Hinde, RA., Berman, CM., editors. *Primate social relationships: An integrated approach*. Oxford: Blackwell Scientific; 1983. p. 93-103.
- Datta SB. The acquisition of dominance among free-ranging rhesus monkey siblings. *Animal Behaviour*. 1988; 36(3):754–772.
- Datta SB, Beauchamp G. Effects of group demography on dominance relationships among female primates. I. Mother-daughter and sister-sister relations. *American Naturalist*. 1991:201–226.
- de Vries H. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*. 1998; 55(4):827–843. [PubMed: 9632471]
- de Waal F, Luttrell LM. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stump-tail monkeys. *American Journal of Primatology*. 1989; 19(2):83–109.
- de Waal FB, Luttrell LM. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethology and Sociobiology*. 1988; 9(2–4):101–118.
- de Waal FBM, Luttrell LM. The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. *American Journal of Primatology*. 1985; 9(2):73–85.
- Ehardt CL, Bernstein IS. Matrilineal overthrows in rhesus monkey groups. *International Journal of Primatology*. 1986; 7(2):157–181.
- Ehardt, CL., Bernstein, IS. Conflict intervention behaviour by adult male macaques: structural and functional aspects. In: Harcourt, AH., de Waal, FB., editors. *Coalitions and alliances in humans and other animals*. Oxford: Oxford University Press; 1992. p. 83-111.

- Engh AL, Hoffmeier RR, Seyfarth RM, Cheney DL. O brother, where art thou? The varying influence of older siblings in rank acquisition by female baboons. *Behavioral Ecology and Sociobiology*. 2009; 64(1):97–104.
- Flack JC, Girvan M, de Waal FBM, Krakauer DC. Policing stabilizes construction of social niches in primates. *Nature*. 2006; 439(7075):426–429. [PubMed: 16437106]
- Fushing H, McAssey MP, Beisner B, McCowan B. Ranking network of a captive rhesus macaque society: a sophisticated corporative kingdom. *PLoS ONE*. 2011; 6(3):e17817.doi: 10.1371/journal.pone.0017817 [PubMed: 21423627]
- Grueber C, Nakagawa S, Laws R, Jamieson I. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*. 2011; 24(4):699–711. [PubMed: 21272107]
- Hardin, JW., Hilbe, J. Generalized linear models and extensions. 2. College Station, TX: Stata Press; 2007.
- Holekamp KE, Smale L. Dominance acquisition during mammalian social development: the “inheritance” of maternal rank. *American Zoologist*. 1991; 31(2):306–317.
- Horrocks J, Hunte W. Maternal rank and offspring rank in vervet monkeys: an appraisal of the mechanisms of rank acquisition. *Animal Behaviour*. 1983; 31(3):772–782.
- Hrdy SB, Hrdy DB. Hierarchical relations among female Hanuman langurs (Primates: Colobinae, *Presbytis entellus*). *Science*. 1976; 193(4256):913–915. [PubMed: 17753641]
- Hunte W, Horrocks J. Kin and non-kin interventions in the aggressive disputes of vervet monkeys. *Behavioral Ecology and Sociobiology*. 1987; 20(4):257–263.
- Isbell LA, Pruett JD. Differences between vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) in agonistic interactions between adult females. *International Journal of Primatology*. 1998; 19(5):837–855.
- Isbell LA, Young TP. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour*. 2002:177–202.
- Johnson JA. Dominance rank in juvenile olive baboons, *Papio anubis*: the influence of gender, size, maternal rank and orphaning. *Animal Behaviour*. 1987; 35(6):1694–1708.
- Jones CB. The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous neotropical primate. *Primates*. 1980; 21(3):389–405.
- Kaufmann JH. On the definitions and functions of dominance and territoriality. *Biological Reviews*. 1983; 58(1):1–20.
- Kawai M. On the rank system in a natural group of Japanese monkeys (I). *Primates*. 1958; 1(2):111–130.
- Langergraber, K. Cooperation among kin. In: Mitani, JC, Call, J, Kappeler, PM, Palombit, RA., Silk, JB., editors. *The evolution of primate societies*. Chicago, IL: University of Chicago Press; 2012. p. 491–513.
- Lea AJ, Learn NH, Theus MJ, Altmann J, Alberts SC. Complex sources of variance in female dominance rank in a nepotistic society. *Animal Behaviour*. 2014; 94:87–99. [PubMed: 26997663]
- Lee, P. Context-specific unpredictability in dominance interactions. In: Hinde, RA., Berman, CM., editors. *Primate social relationships: An integrated approach*. Oxford: Blackwell Scientific; 1983.
- Lee P, Oliver J. Competition, dominance and the acquisition of rank in juvenile yellow baboons (*Papio cynocephalus*). *Animal Behaviour*. 1979; 27:576–585.
- McCowan B, Beisner BA, Capitanio JP, Jackson ME, Cameron AN, Seil S, Fushing H. Network stability is a balancing act of personality, power, and conflict dynamics in rhesus macaque societies. *PLoS ONE*. 2011; 6(8):e22350. [PubMed: 21857922]
- Missakian EA. Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. *Primates*. 1972; 13(2):169–180.
- Moore J. Dispersal, nepotism, and primate social behavior. *International Journal of Primatology*. 1992; 13(4):361–378.
- Muggeo, VMR. segmented: an R Package to Fit Regression Models with Broken-Line Relationships. 2008. Retrieved from <http://cran.r-project.org/doc/Rnews/>

- Netto, W., Van Hooff, J. Conflict interference and the development of dominance relationships in immature *Macaca fascicularis*. In: Else, JG., Lee, PC., editors. Primate ontogeny, cognition and social behaviour. Cambridge: Cambridge University Press; 1986. p. 291-300.
- Oates-O'Brien RS, Farver TB, Anderson-Vicino KC, McCowan B, Lerche NW. Predictors of matrilineal overthrows in large captive breeding groups of rhesus macaques (*Macaca mulatta*). Journal of the American Association for Laboratory Animal Science: JAALAS. 2010; 49(2):196. [PubMed: 20353695]
- Parker GA. Assessment strategy and the evolution of fighting behaviour. Journal of Theoretical Biology. 1974; 47(1):223–243. [PubMed: 4477626]
- Petit O, Abegg C, Thierry B. A comparative study of aggression and conciliation in three cercopitheciine monkeys (*Macaca fuscata*, *Macaca nigra*, *Papio papio*). Behaviour. 1997; 134(5): 415–432. doi: <http://dx.doi.org/10.1163/156853997X00610>.
- R Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. 2013. Retrieved from <http://www.R-project.org/>
- Rabe-Hesketh, S., Skrondal, A. Multilevel and longitudinal modeling using Stata: Categorical responses, counts, and survival. 3. Vol. 2. College Station, Tex: Stata Press Publication; 2012.
- Raleigh MJ, McGuire MT, Brammer GL, Pollack DB, Yuwiler A. Serotonergic mechanisms promote dominance acquisition in adult male vervet monkeys. Brain Research. 1991; 559(2):181–190. [PubMed: 1794096]
- Richards SA. Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology. 2005; 86(10):2805–2814.
- Sade, DS. Determinants of dominance in a group of free-ranging rhesus monkeys. In: Altmann, SA., Altmann, A., editors. Social communication among primates. Chicago: University of Chicago Press; 1967. p. 99-114.
- Sapolsky RM, Share LJ. Rank-related differences in cardiovascular function among wild baboons: Role of sensitivity to glucocorticoids. American Journal of Primatology. 1994; 32(4):261–275.
- Sebastian SO. Using individual attributes to predict hierarchical position in a *Macaca sylvanus* group at 'La forêt des singes', Rocamadour. Behavioural Processes. 2015; 111:109–117. [PubMed: 25562191]
- Silk JB, Samuels A, Rodman PS. Hierarchical organization of female *Macaca radiata* in captivity. Primates. 1981; 22(1):84–95.
- Small MF. Body fat, rank, and nutritional status in a captive group of rhesus macaques. International Journal of Primatology. 1981; 2(1):91–95.
- Sprague DS. Age, dominance rank, natal status, and tenure among male macaques. American Journal of Physical Anthropology. 1998; 105(4):511–521. [PubMed: 9584892]
- Sterck EH, Watts DP, van Schaik CP. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology. 1997; 41(5):291–309.
- Symonds MR, Moussalli A. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology. 2011; 65(1):13–21.
- Thierry B. Patterns of agonistic interactions in three species of macaque (*Macaca mulatta*, *M fascicularis*, *M tonkeana*). Aggressive Behavior. 1985; 11(3):223–233.
- Van Noordwijk MA, Van Schaik CP. Competition among female long-tailed macaques, *Macaca fascicularis*. Animal Behaviour. 1987; 35(2):577–589.
- van Schaik, CP. The ecology of social relationships amongst female primates. In: Hawkes, K.O'Connell, JF., Jones, NB., editors. Comparative socioecology: The behavioural ecology of humans and other mammals. Oxford: Blackwell; 1989. p. 195-218.
- Wilson M, Gordon T, Blank M, Collins D. Timing of sexual maturity in female rhesus monkeys (*Macaca mulatta*) housed outdoors. Journal of Reproduction and Fertility. 1984; 70(2):625–633. [PubMed: 6422036]
- Wrangham RW. An ecological model of female-bonded primate groups. Behaviour. 1980:262–300.

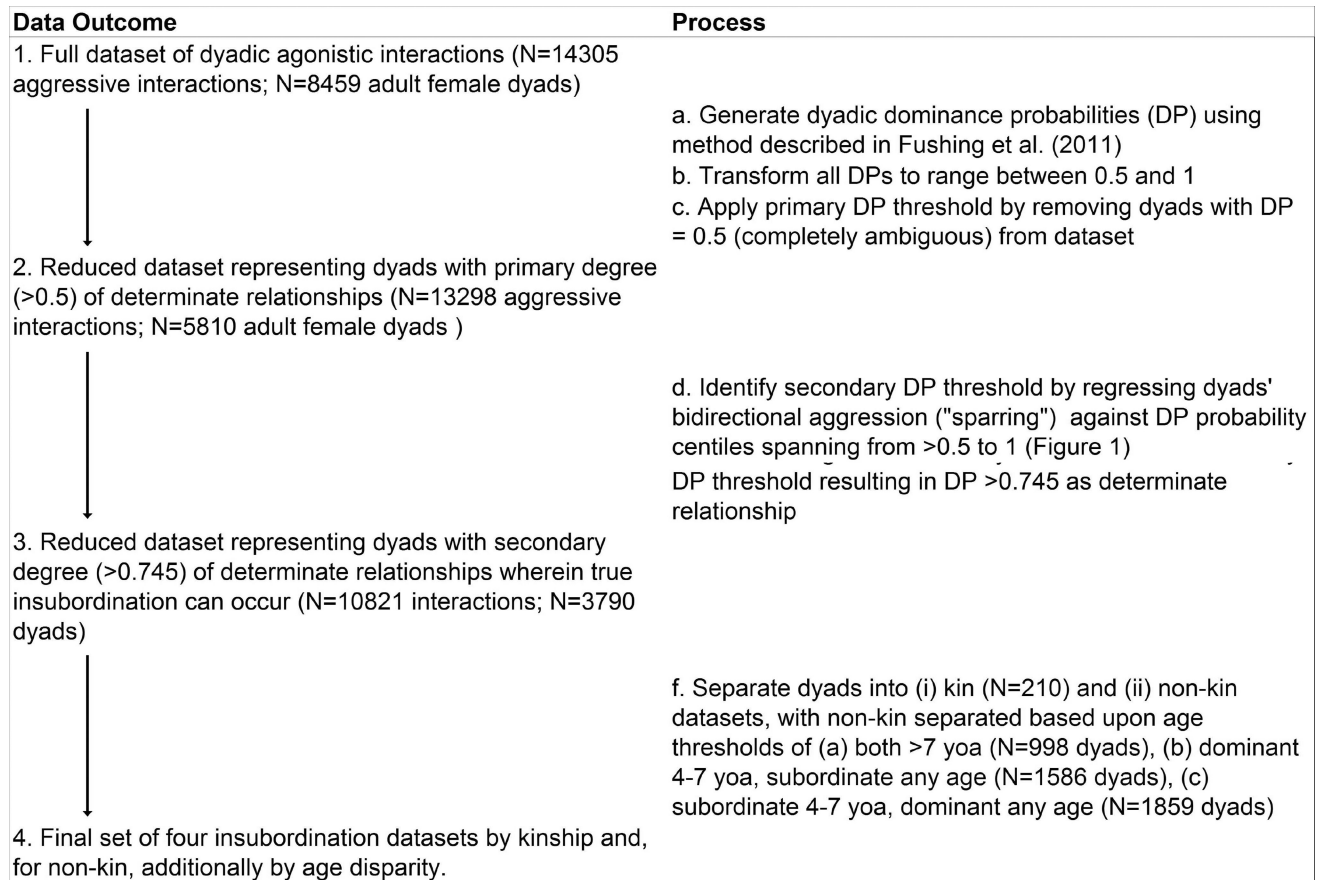


Fig. 1.
Process for refining and creating subsets of data for analyses.

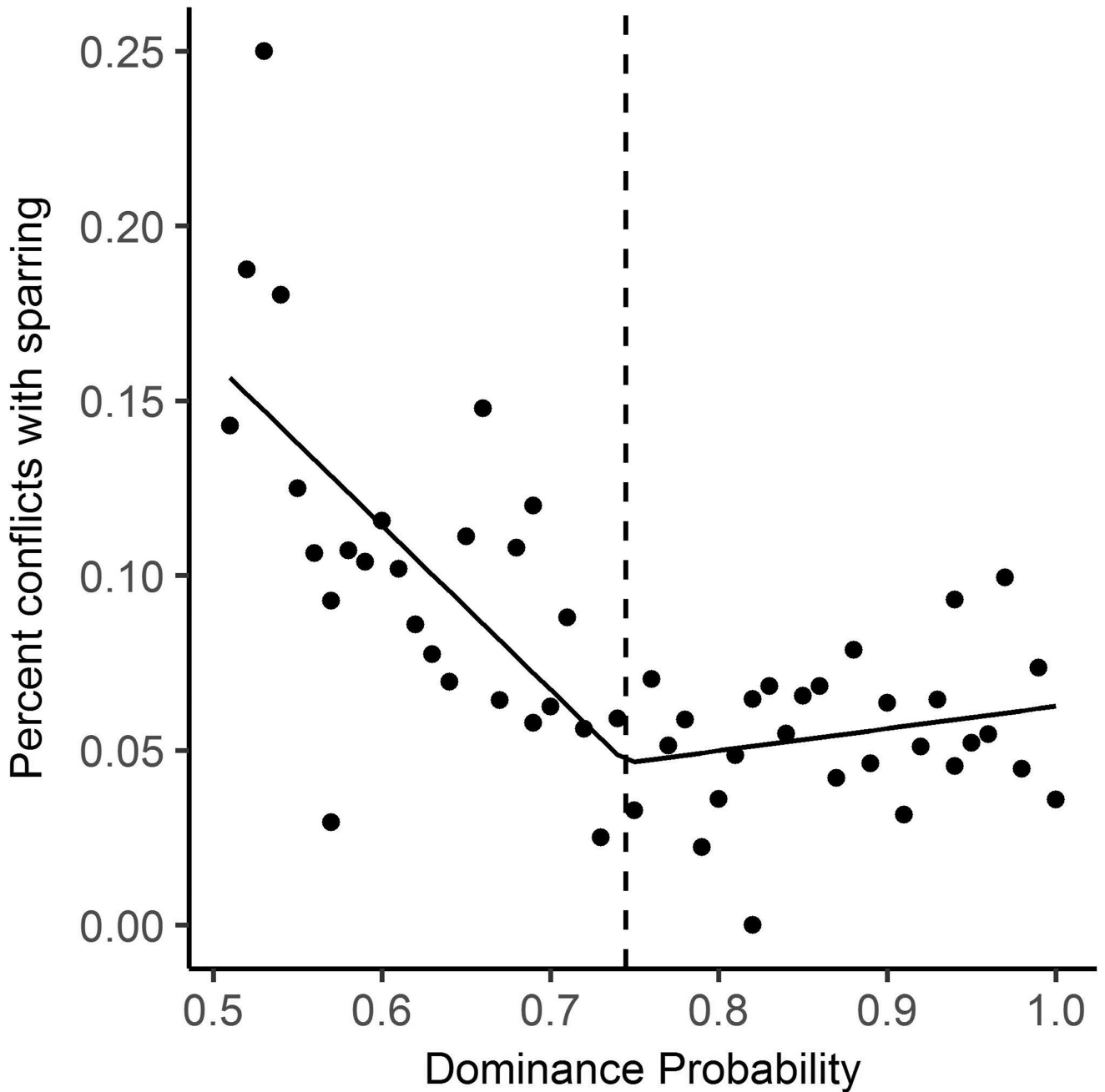


Fig. 2.

Segmented regression of percent of conflicts with sparring (or bidirectional aggression) against dominance probability for all adult female dyads in the study groups. The dashed line indicates the dominance probability value (0.745) that defines the two line segments. Dyads with dominance probability values to the left of the dashed line have a dominance relationship that is more or less ambiguous and contra-hierarchical aggression among these dyads should not be considered true insubordination. Dyads with dominance probability values to the right of the dashed line have determinate dominance relationships and contra-hierarchical aggression among them can be characterized as insubordinate.

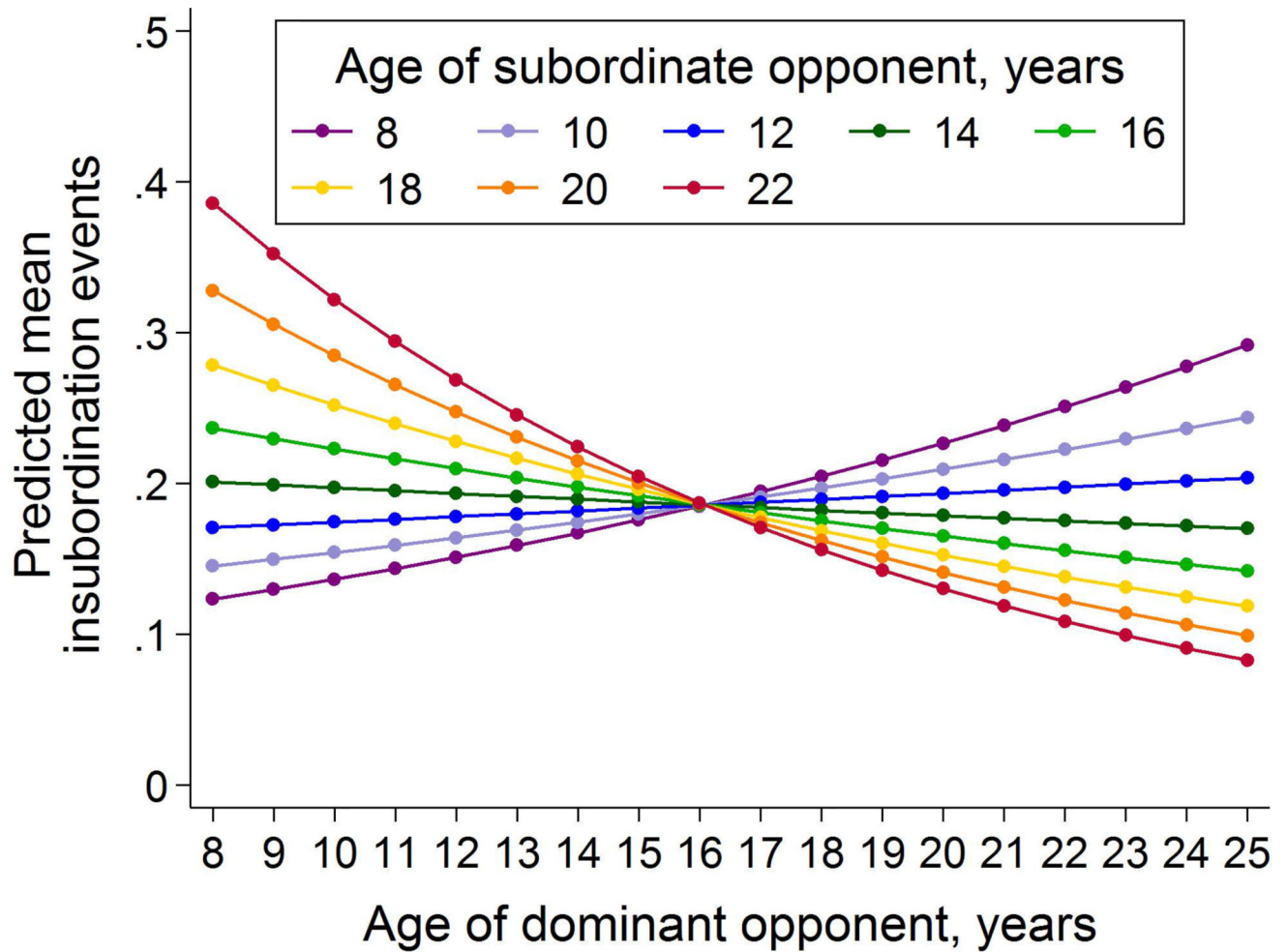


Fig. 3.

The mean count of insubordination events predicted by the interaction of the ages of the subordinate and dominant opponents, given that the dyad is not kin and both are full adults (> 7 yoa).

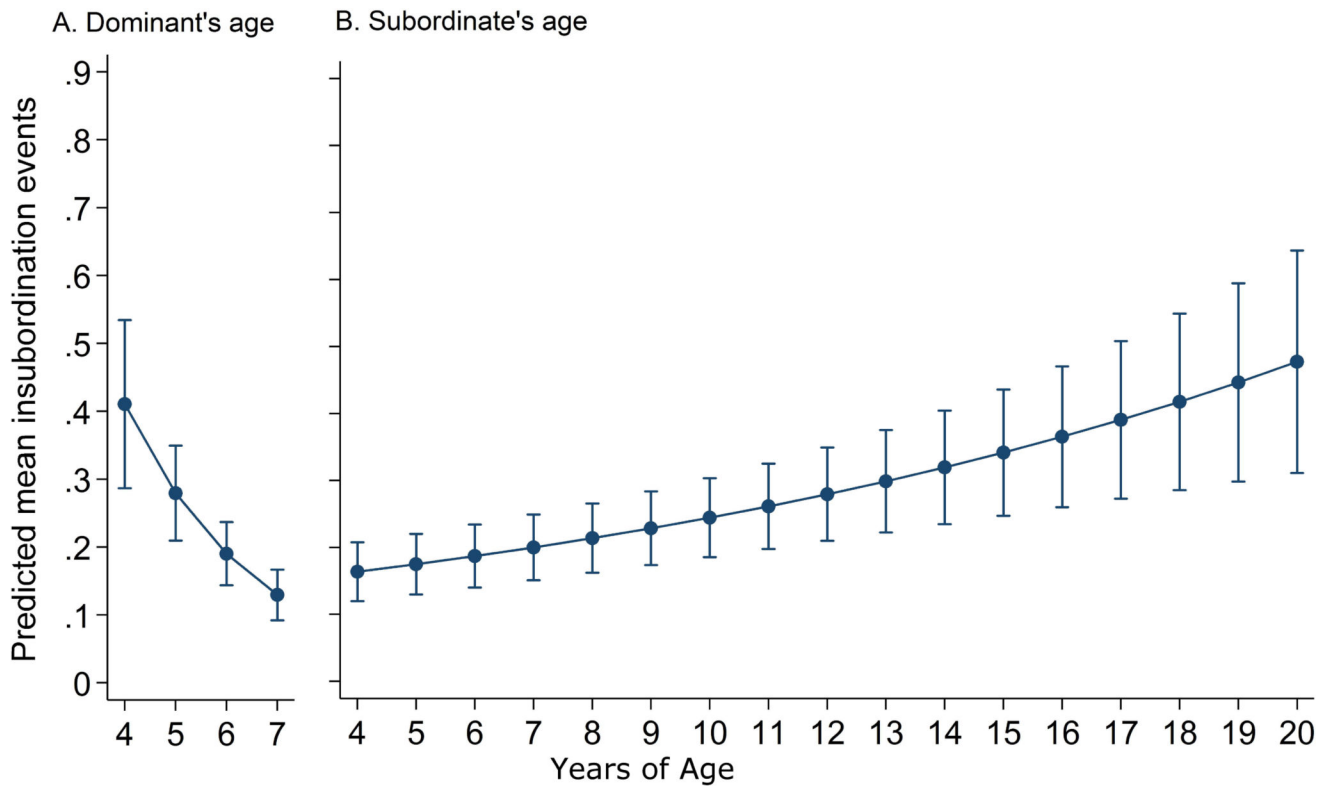


Fig. 4.

The mean count of insubordination events, given that the dyad is not kin and the dominant is a young adult (4–7 yoa), predicted by: A) the age of the dominant opponent, and B) the age of the subordinate opponent. There is no interaction between opponent ages.

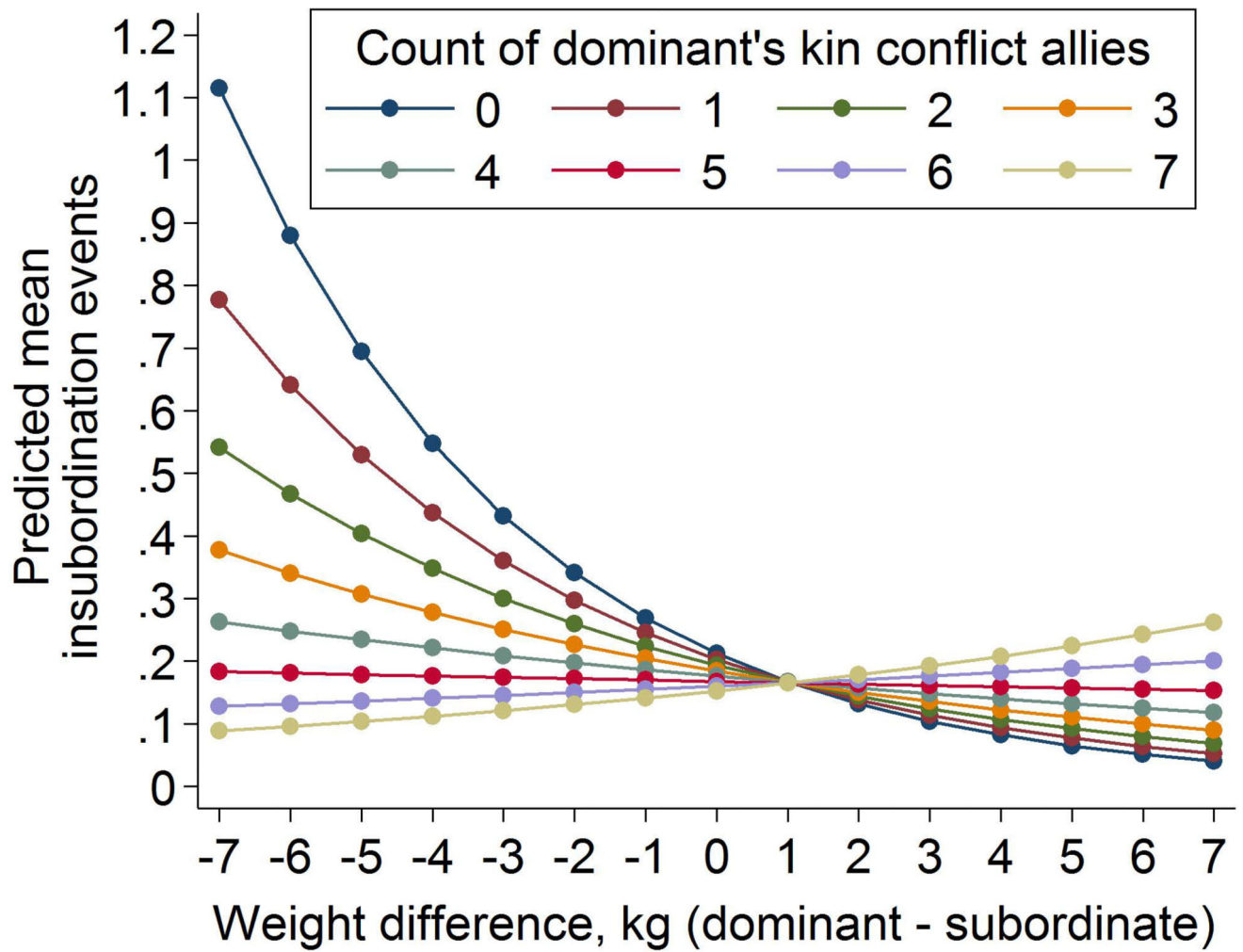


Fig. 5. The mean count of insubordination events predicted by the interaction of body weight difference of the dyad (dominant kg – subordinate kg) and the dominant's number of kin allies, given that the dyad is not kin and both are full adults (> 7 yoa).

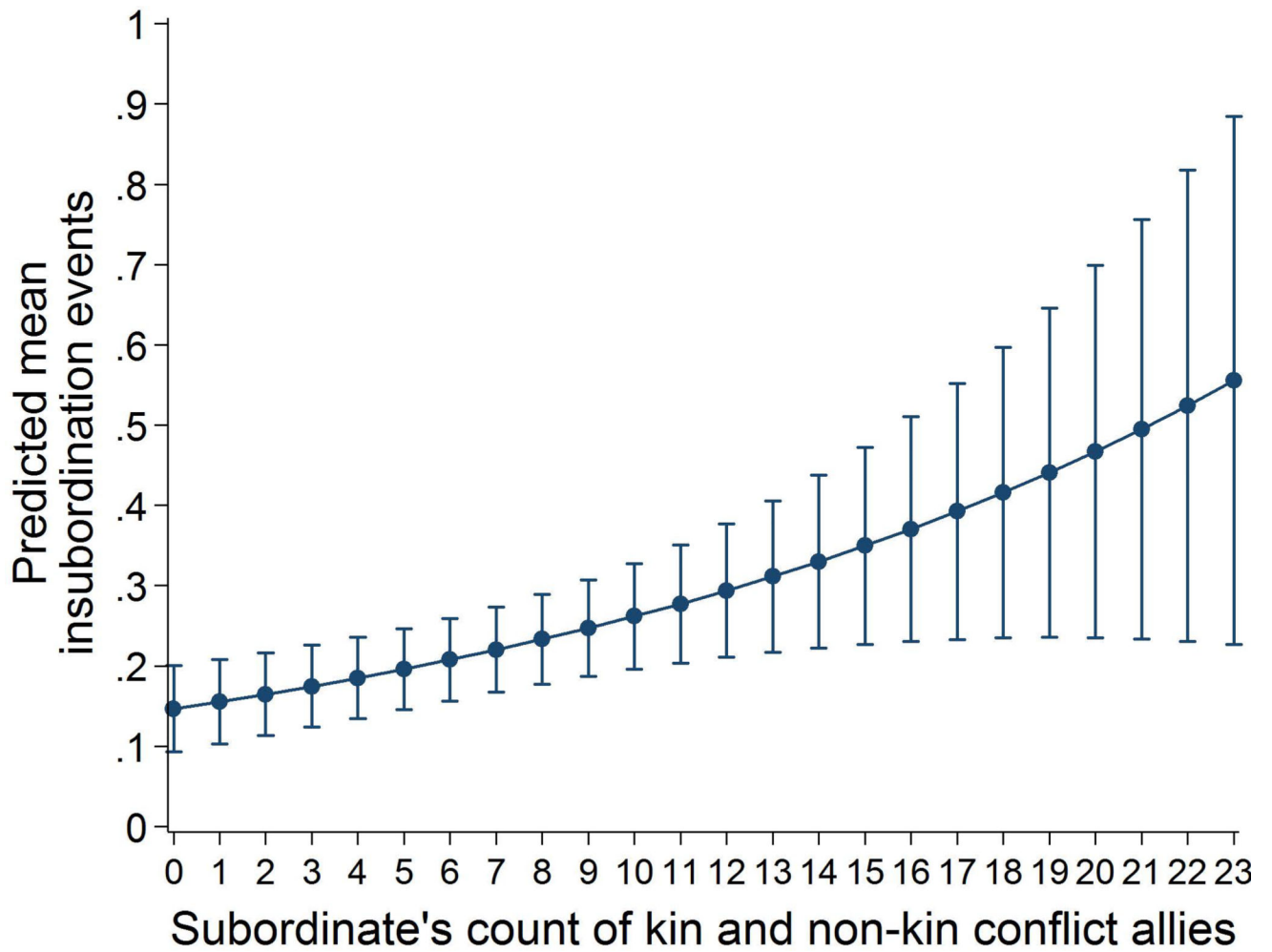


Fig. 6.

The mean count of insubordination events predicted by the total ally count of the subordinate (both kin and non-kin allies), given that the dyad is not kin and the dominant is a young adult (4–7 yoa).

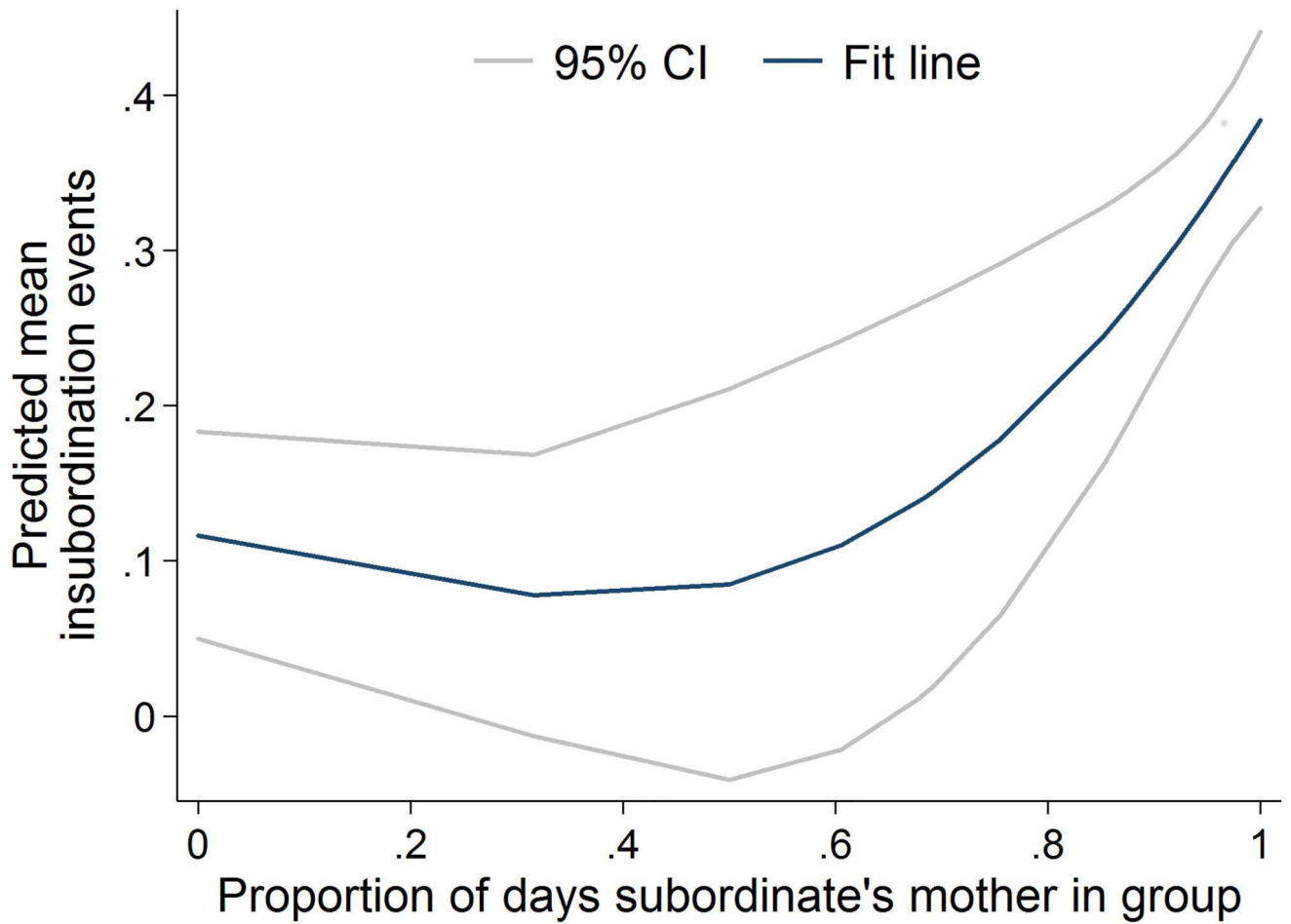


Fig. 7. The mean count of insubordination events, given that the dyad is kin, predicted by the proportion of data collection days that the subordinate's mother was present in the group.

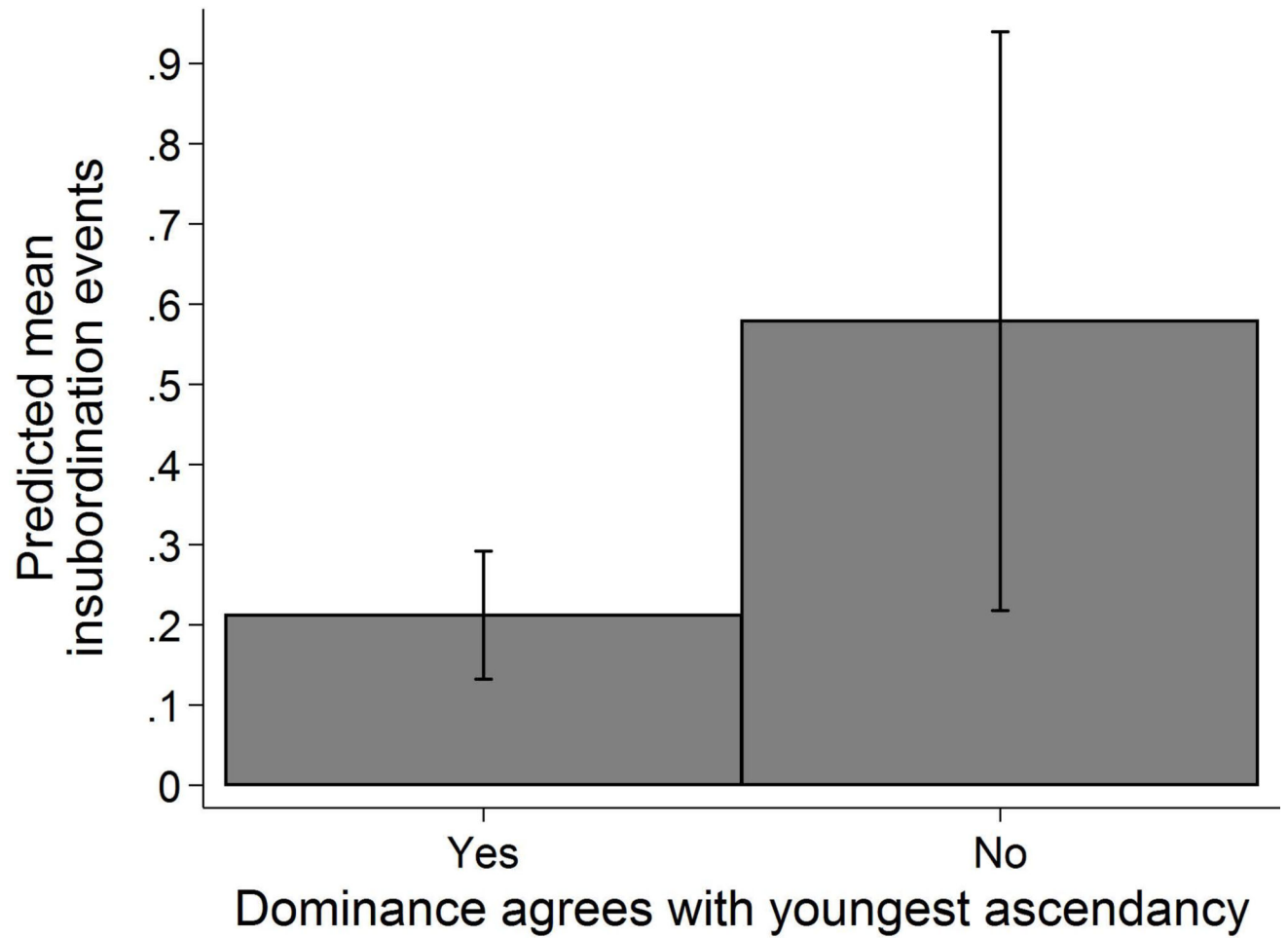


Fig. 8.

The mean count of insubordination events, given that the dyad is kin, predicted by whether the dyad's dominance relationship is consistent with the direction expected according to the rule of youngest ascendancy (i.e., as predicted based on birth order among a matriarch's female descendants).

Table 1

Attributes of groups and data collected

Group	Average group size	Females >3 years old	Observation hours
1	178	51	182
5	137	59	211
8	157	76	209
10	165	68	178
14	108	38	203
18	197	65	176

Author Manuscript

Author Manuscript

Author Manuscript

Author Manuscript

Table 2

Description of variables tested

Variable	Description
Challenges (outcome)	For each dyad, count of interactions wherein the subordinate animal behaved aggressively towards the dominant.
Conflicts (offset)	For each dyad, count of interactions wherein one or both animals behaved aggressively towards the other.
Group (random effect)	The social group to which the subjects belonged (N=6).
Age ¹	Age in years at the start of data collection. Exact date of birth is on record for all subjects as part of routine colony management. Absolute age, rather than age difference, was used in order to test hypotheses concerning the effects of developmental stage on insubordination.
Presence of mother ¹	The proportion of data collection days wherein the subject's mother co-resided with her in the group. Records of housing history, accurate to the day, were used to ascertain whether a subject's mother was present for each day a group was observed. Parentage was determined through genetic testing. In cases where a subject was known to be reared by an adoptive mother, the adoptive, not genetic, mother was used for this measure. Because groups were housed in 0.2 ha enclosures with full visibility and easy access to all areas, mothers were able to continuously monitor the social encounters of their offspring at all times. Therefore we assume that if a mother is present in the group on a given day, she can be considered 'present' for any conflicts involving her daughter on that day.
Weight difference	For each dyad, the dominant opponent's weight minus the subordinate opponent's weight (kg). Weights were recorded every six months for all animals in each group during semiannual physical exams. Weights collected closest to the beginning of data collection were used for this study. Weight difference was used instead of the absolute weights of each subject because it was sufficient to test our hypotheses and conserves degrees of freedom.
Relative dominance rank ¹	Animals were assigned sequential dominance ranks, with 1 being the highest ranking, using dominance probability matrices (see Methods and Fushing et al. 2011). For each subject, relative rank was quantified as ordinal rank divided by the maximum rank for each group to control for group size. Low values indicate high rank. Rank was included as a control variable and not to test specific hypotheses.
Relatedness ²	Since all subjects and generations of their ancestors were born into captivity and extensively monitored and tested, all maternal kin relationships were known through observation and blood analysis. Known adoptive mothers were treated as genetic mothers for this analysis. Maternal genetic relatedness coefficients were calculated using a maternal kin network. Each pathway between two maternally related animals represented a 50% reduction in genetic relatedness. Thus mothers and daughters had $r = 0.5$; sisters, $r = 0.25$; maternal aunts/nieces, $r = 0.125$. Dyads were only considered maternal kin when they were at least 0.0625 related. This level of relatedness has been identified as a threshold for differential social responsiveness to kin versus non-kin (Rendall et al., 1996).
Allies ¹	Count of co-aggressors during the study period. Co-aggressors were defined as animals over three years of age (male or female) who participated in mutual aggression towards a target with each subject in any context at least once (e.g. partial interventions, mobbing). Three types of allies were counted for each opponent, based on maternal relatedness (see Relatedness above): maternal kin allies, non-kin allies, and all allies (kin + non-kin allies). Due to potential issues with collinearity, the 'all allies' variable was not included in the same model with kin allies or non-kin allies.
Youngest ascendancy violation ²	Youngest ascendancy was violated for a given dyad if the observed direction of dominance was different from expected. Expected ranks were deduced by applying the rule of youngest ascendancy to pedigree data going back generations to the matriarch of each matriline (the founding female that each matriline member is related to). Starting from the matriarch, each of her daughters rank below her in age-inverse order, and all descendants of each daughter rank together with their mother.
Interactions tested	Dominant's age (years) x Subordinate's age (years) Proportion of days mother present x Youngest ascendancy violation ^{1,2} Weight difference x Count of all allies (kin + non-kin) ¹ Weight difference x Count of kin allies ¹ Weight difference x Count of non-kin allies ¹

¹Included as a separate variable for both the dominant and subordinate opponent

²Variable was only tested for kin model

Table 3

Summary of variables retained, or not, in best model set based on model selection results.

Variable by type	Kin subset		Non-kin subsets	
	Any age adult	Both full adults	Dominant is a young adult	Subordinate is a young adult
Intrinsic factors				
Dominant's age	-	+	+	+
Subordinate's age	-	+	+	+
Age interaction	-	+	-	-
Maternal relatedness	-	n/a	n/a	n/a
Weight disparity	n/a	+	n/a	n/a
Extrinsic factors				
Dominant's maternal kin allies	-	+	-	-
Subordinate's maternal kin allies	-	-	-	-
Dominant's non-kin allies	-	-	-	-
Subordinate's non-kin allies	+	-	+	+
Dominant's total allies	-	-	-	-
Subordinate's total allies	-	+	+	+
Presence of dominant's mother	-	-	+	-
Presence of subordinate's mother	+	-	-	+
Violation of youngest ascendency	+	n/a	n/a	n/a
Interactions tested				
Dominant's age (years) x Subordinate's age (years)	-	+	-	-
Proportion of days dominant's mother present x Youngest ascendency violation	-	n/a	n/a	n/a
Proportion of days subordinate's mother present x Youngest ascendency violation	-	n/a	n/a	n/a
Weight difference x Count of all dominant's allies	n/a	-	n/a	n/a
Weight difference x Count of dominant's kin allies	n/a	+	n/a	n/a
Weight difference x Count of dominant's non-kin allies	n/a	-	n/a	n/a
Weight difference x Count of all subordinate's allies	n/a	-	n/a	n/a
Weight difference x Count of subordinate's kin allies	n/a	-	n/a	n/a
Weight difference x Count of subordinate's non-kin allies	n/a	-	n/a	n/a

+ Variable was retained in best model set

- Variable was not retained in best model set

n/a Variable was not appropriate for testing in that subset

Table 4

Best-fit model comparison for all data subsets

4A. Model comparison for insubordinate aggression among dyads wherein both females are >7 yoa

Model	AIC	dAIC	Model likelihood	Model weight	Evidence ratio
Weight diff + Sub all allies + Dom rank + Dom age + Sub age + Dom age x Sub age + Dom kin allies + Weight diff x Dom kin allies	933.06	0.00	1.00	0.58	1.00
Weight diff + Sub all allies + Dom rank + Dom kin allies + Weight diff x Dom kin allies	935.23	2.16	0.34	0.20	2.95
Weight diff + Sub all allies + Dom age + Sub age + Dom age x Sub age + Dom kin allies + Weight diff x Dom kin allies	935.60	2.54	0.28	0.16	3.55
Weight diff + Sub all allies + Dom rank + Dom age + Sub age + Dom age x Sub age	937.52	4.45	0.11	0.06	9.26

4B. Model comparison for insubordinate aggression among dyads wherein the dominant is 4–7 yoa

Model	AIC	dAIC	Model likelihood	Model weight	Evidence ratio
Dom age + Sub age + Sub all allies + Dom rank + Sub rank + Presence of dom's mother	1694.28	0.00	1.00	0.49	1.00
Dom age + Sub age + Sub non-kin allies + Dom rank + Sub rank + Presence of dom's mother	1695.86	1.58	0.45	0.22	2.20
Dom age + Sub age + Sub all allies + Dom rank + Sub rank	1696.59	2.31	0.31	0.15	3.18
Dom age + Sub age + Sub all allies + Dom rank + Presence of dom's mother	1697.67	3.39	0.18	0.09	5.45
Dom age + Sub age + Sub non-kin allies + Dom rank + Sub rank	1698.74	4.46	0.11	0.05	9.31

4C. Model comparison for insubordinate aggression among dyads wherein the subordinate is 4–7 yoa

Model	AIC	dAIC	Model likelihood	Model weight	Evidence ratio
Dom age + Sub age + Sub all allies + Dom rank + Sub rank	1386.99	0.00	1.00	0.55	1.00
Dom age + Sub age + Sub all allies + Dom rank + Presence of sub's mother	1388.91	1.92	0.38	0.21	2.61
Dom age + Sub age + Sub non-kin allies + Dom rank + Sub rank	1389.30	2.31	0.31	0.17	3.18
Dom age + Sub age + Sub all allies + Dom rank	1391.03	4.04	0.13	0.07	7.56

4D. Model comparison for insubordinate aggression among kin dyads

Model	AIC	dAIC	Model likelihood	Model weight	Evidence ratio
Sub's count of non-kin allies + Presence of sub's mother + Youngest ascendancy violation	228.19	0.00	1.00	1.73	0.00
Presence of sub's mother + Youngest ascendancy violation	230.46	2.27	0.32	0.55	0.00

Random effect: Group
Dom = dominant opponent
Sub = subordinate opponent
Weight diff = weight difference

Author Manuscript

Author Manuscript

Author Manuscript

Author Manuscript

Model estimates for intrinsic and extrinsic characteristics influencing the incidence of insubordinate aggression among non-kin dyads of three age classes (both opponents > 7 yoa, subordinate opponent 4–7 yoa, dominant opponent 4–7 yoa)

Table 5

<i>5A. Model weights, variate weights and incidence rate ratios (IRRs) with standard errors for the set of candidate models for non-kin dyads wherein both opponents are >7 yoa</i>															
AIC	Model Weight	Intercept	Weight difference	Dom rank	Sub rank	Dom age	Sub age	Dom age x Sub age	Dom kin allies	Sub all allies	Sub non-kin allies	Dom mother presence	Sub mother presence	WD x Dom kin allies	Random effect (group)
933.07	0.579	0.004 (0.003)	0.789 (0.056)	2.391 (0.970)		1.140 (0.060)	1.176 (0.071)	0.990 (0.004)	1.046 (0.018)	1.091 (0.021)				1.046 (0.018)	0.020 (0.040)
935.23	0.196	0.032 (0.010)	0.775 (0.056)	2.434 (0.992)					0.962 (0.044)	1.097 (0.044)				1.049 (0.018)	0.007 (0.029)
935.60	0.163	0.006 (0.005)	0.786 (0.056)			1.140 (0.060)	1.178 (0.069)	0.990 (0.004)	0.925 (0.041)	1.085 (0.059)				1.047 (0.018)	0.021 (0.039)
937.52	0.062	0.003 (0.002)	0.930 (0.030)	3.030 (1.173)		1.144 (0.061)	1.185 (0.071)	0.990 (0.004)		1.090 (0.022)					0.063 (0.065)
Variate weight:				1.000	0.837	0.804	0.804	0.804	0.938	1.000				0.938	
<i>5B. Model weights, variate weights and incidence rate ratios (IRRs) with standard errors for the set of candidate models for non-kin dyads wherein the subordinate is 4–7 yoa</i>															
AIC	Model Weight	Intercept	Weight difference	Dom rank	Sub rank	Dom age	Sub age	Dom age x Sub age	Dom kin allies	Sub all allies	Sub non-kin allies	Dom mother presence	Sub mother presence	WD x Dom kin allies	Random effect (group)
1386.99	0.546	0.017 (0.009)	n/a	7.450 (2.875)	0.379 (0.150)	0.936 (0.016)	1.200 (0.083)			1.081 (0.029)				n/a	0.027 (0.030)
1388.91	0.209	0.007 (0.004)	n/a	4.792 (1.532)		0.934 (0.016)	1.187 (0.082)			1.102 (0.028)				1.472 (0.280)	0.015 (0.023)
1389.30	0.172	0.026 (0.012)	n/a	7.021 (2.710)	0.332 (0.128)	0.935 (0.016)	1.188 (0.083)				1.081 (0.034)			n/a	0.036 (0.036)
1391.03	0.072	0.011 (0.005)	n/a	4.481 (1.428)	0.011 (0.005)	0.933 (0.016)	1.161 (0.079)			1.103 (0.028)				n/a	0.031 (0.032)
Variate weight:				1.000	0.791	1.000	1.000		0.828	0.172			0.209		
<i>5C. Model weights, variate weights and incidence rate ratios (IRRs) with standard errors for the set of candidate models for non-kin dyads wherein the dominant is 4–7 yoa</i>															
AIC	Model Weight	Intercept	Weight difference	Dom rank	Sub rank	Dom age	Sub age	Dom age x Sub age	Dom kin allies	Sub all allies	Sub non-kin allies	Dom mother presence	Sub mother presence	WD x Dom kin allies	Random effect (group)
1694.28	0.485	0.344 (0.155)	n/a	3.744 (1.139)	0.493 (0.151)	0.681 (0.039)	1.069 (0.013)			1.060 (0.019)		0.758 (0.100)		n/a	0.050 (0.044)
1695.86	0.221	0.457 (0.193)	n/a	3.731 (1.133)	0.420 (0.123)	0.676 (0.039)	1.071 (0.013)				1.065 (0.023)	0.746 (0.098)		n/a	0.053 (0.046)
1696.59	0.153	0.308 (0.140)	n/a	3.502 (1.069)	0.485 (0.149)	0.676 (0.039)	1.068 (0.013)			1.061 (0.019)				n/a	0.047 (0.044)
1697.67	0.089	0.209 (0.083)	n/a	2.552 (0.640)		0.682 (0.039)	1.071 (0.013)			1.075 (0.018)		0.753 (0.099)		n/a	0.044 (0.039)
1698.74	0.052	0.414 (0.176)	n/a	3.474 (1.060)	0.409 (0.120)	0.670 (0.039)	1.070 (0.013)				1.064 (0.023)			n/a	0.052 (0.046)

5C. Model weights, variate weights and incidence rate ratios (IRRs) with standard errors for the set of candidate models for non-kin dyads wherein the dominant is 4-7 yoa

AIC	Model Weight	Intercept	Weight difference	Dom rank	Sub rank	Dom age	Sub age	Dom age x Sub age	Dom kin allies	Sub all allies	Sub non-kin allies	Dom mother presence	Sub mother presence	WD x Dom kin allies	Random effect (group)
	Variate weight:			1.000	0.911	1.000	1.000		0.727		0.273	0.795			

Dom = dominant opponent

Sub = subordinate opponent

WD = weight difference

n/a = Variable was not tested in this subset

Model weights, variate weights and incidence rate ratios (IRR) for best-fit models of insubordinate aggression among kin dyads

Table 6

AIC	Model weight	Intercept	Sub Mother Presence	Youngest ascendancy violation	Sub non-kin allies	Random effect (Group)
228.190	0.757	0.012 (0.006)	2.928 (1.248)	2.727 (1.002)	1.160 (0.083)	6.77E-33 (3E-17)
230.464	0.243	0.023 (0.009)	3.039 (1.296)	2.515 (0.931)		4.17E-34 (4.82E-18)
Variate Weight			1.000	1.000	0.757	

Dom = dominant opponent

Sub = subordinate opponent