

20 **Abstract**

21 Evolutionary theories predict that sibling relationships will reflect a complex balance of
22 cooperative and competitive dynamics. In most mammals, dispersal and death patterns mean that
23 sibling relationships occur in a relatively narrow window during development, and/or only with
24 same-sex individuals. Besides humans, one notable exception are mountain gorillas, in which non-
25 sex biased dispersal, relatively stable group composition, and the long reproductive tenures of alpha
26 males mean that animals routinely reside with both same and opposite-sex, and full and half siblings,
27 throughout their lives. Using nearly 40,000 hours of observation data collected over 14 years on 699
28 sibling and 1258 non-sibling pairs of wild mountain gorillas, we demonstrate that individuals have
29 strong affiliative preferences for full and maternal siblings over paternal siblings or unrelated
30 animals, consistent with an inability to discriminate paternal kin. Intriguingly, however, aggression
31 data imply the opposite. Aggression rates were statistically indistinguishable among all types of dyads
32 except one: in mixed-sex dyads, non-siblings engaged in substantially more aggression than siblings
33 of any type. This pattern suggests mountain gorillas may be capable of distinguishing paternal kin,
34 but nonetheless choose not to affiliate with them over non-kin. A preference for maternal kin
35 occurs despite gorillas not possessing low male reproductive skew, the key characteristic believed to
36 underlie such biases. These results call into question reasons for strong maternal kin biases when
37 paternal kin are identifiable, familiar, and similarly likely to be long-term social partners, and suggest
38 behavioral mismatches at play during a transitional period in mountain gorilla society.

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40 **Key words:** paternal kin, maternal kin, kin selection, kin recognition, primatology

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43 **Introduction**

44 In humans and non-human animals alike, sibling social relationships are marked by
45 continuous dynamics of conflict and cooperation that begin before birth (Trivers, 1974), and can
46 persist throughout an entire lifespan, with important fitness consequences for the individuals
47 involved (Lu, 2007; Hudson & Trillmich, 2008; Nitsch et al., 2013). While classical frameworks of
48 sibling interactions emphasized competition among brood- or litter-mates for limited parental
49 resources during times of dependency (e.g. Mock & Parker, 1997), subsequent developments across
50 numerous academic disciplines (**demography**: e.g. Sear & Mace, 2008; Nitsch et al., 2013;
51 **sociology**: e.g. Steelman et al., 2002; Lu, 2007; **behavioral ecology**: e.g. Silk, 2002; Hudson &
52 Trillmich, 2008; **developmental psychology**: e.g. Lamb et al., 2014) have explored the full arc of
53 sibling competition and cooperation across the lifespan and demonstrated the complexity and
54 diversity inherent to sibling relationships. In understanding the evolution of human sibling
55 relationships in particular, comparative studies of our primate cousins have identified a number of
56 factors predictive of how siblings cooperate and compete. Inconsistent results within and between
57 species, along with the remarkable flexibility of human social systems, however, limits the
58 translational value of many primate models. Here, we address these gaps by presenting an extensive
59 longitudinal study of wild mountain gorillas (*Gorilla beringei beringei*), an endangered ape whose
60 unique, flexible social structure serves as a valuable comparative model to humans.

61 Classic models of kin selection predict that the social/mating structure of animal groups
62 creates patterns of relatedness between group members, which then selects for kin recognition
63 mechanisms that manifest in differences in cooperative and/or affiliative behavior (Hamilton, 1964;
64 Grafen, 1990; Mateo, 2015). This straightforward idea has spawned a large body of work on kin
65 discrimination in primates, with notably mixed results. Some studies support the existence of

66 sophisticated kin discrimination (Wu et al., 1980; Smith et al., 2003; Widdig et al., 2002, Pfefferle et
67 al., 2014), while others do not, instead favoring simple familiarity as the primary determinant of
68 interaction patterns (Fredrickson & Sackett, 1984; Schaub, 1996; Erhart et al., 1997; Wikberg et al.,
69 2014; Godoy et al., 2016). Inconsistent evidence has led some to suggest that non-monogamous
70 primates evince matrilineal, but not patrilineal, sibling kin discrimination (Mitani et al., 2000;
71 Chapais, 2001; Langergraber et al., 2007). Yet other perspectives challenge this clean distinction,
72 suggesting that complex interactions between familiarity and kin discrimination structure social
73 bonds across primates (see e.g. Silk, 2002; Widdig et al., 2002; Silk, 2009; Lynch et al., 2017).

74 As one of the main contributors to familiarity, age differences within sibling and non-sibling
75 dyads might influence social dynamics. On one hand, siblings close in age might be more likely to
76 compete for limited parental resources (Tung et al., 2016; Salmon & Hehman, 2021); on the other
77 hand, as longer-lasting co-residents within the same family environment, they might also be expected
78 to form stronger affiliative bonds than siblings distant in age (though, again, this may not apply
79 equally to maternal and paternal sibships; Widdig et al., 2002). It is unclear to what extent age
80 proximity effects are restricted to genetic relatives. Female rhesus macaques appear to bias affiliation
81 towards similarly-aged peers, even when unrelated to them (Widdig et al., 2001). Among female
82 baboons, even in individuals not related through the matriline, dyadic bond strength weakened with
83 increasing age differences; however, when restricting analyses to females unrelated through both the
84 matriline and patriline, effects of age differences attenuated sharply (Smith et al., 2003; Silk et al.,
85 2006). These results once again imply social familiarity (as indexed by age differences) and kin
86 discrimination are both important for predicting sibling relationship qualities (Godoy et al., 2016),
87 though their additive and/or interactive effects remain poorly defined.

88 Finally, the sex makeup of the dyad might influence interaction styles due to the differential
89 benefits males and females receive from interactions with brothers, sisters, and unrelated partners
90 (e.g. Lonsdorf et al., 2018). From the perspective of males, especially in species who engage in
91 aggressive intrasexual competition, other males, brothers included, can represent important allies
92 (e.g. Meikle & Vessey, 1981; Goodall, 1986) or rivals (Daly & Wilson, 1988) during status-striving
93 efforts in adulthood. In either case, assessing physical capacities or formidability would aid in these
94 efforts. Accordingly, rough-and-tumble play between males might serve important functions as a
95 rehearsal for intrasexual competition in adulthood (Gray, 2019), suggesting such a behavior should
96 occur most often in male-male relationships—a prediction supported by research on male-dominant
97 primates (e.g., Brown & Dixson, 2000; Maestripieri & Ross, 2004). While male-male interaction
98 patterns might generally differ from those of other sex configurations, these differences may
99 themselves partially depend on kinship: in chimpanzees, some evidence suggests that fraternal
100 relationships among adolescents and adults are more affiliative and cooperative than relationships
101 between unrelated males (e.g. Mitani, 2009; Sandel et al., 2020). From the female perspective,
102 evidence for fraternal influences on fitness outcomes is mixed: some research suggests no effect,
103 except perhaps in the case of maternal death (Engh et al., 2009), while one demographic study of
104 humans reports benefits of older brothers on women’s lifetime fitness (Nitsch et al., 2013). From
105 the perspective of both males and females, sisters may represent important future alloparental
106 helpers, either for the individual themselves (e.g. Hamilton et al., 1982; Gould, 2000; Hobaiter et al.,
107 2014), or the individual’s offspring (e.g. Johnson et al., 1980; Nishida, 1983; but see Silk et al., 2006),
108 and thus cultivating relationships with sisters via affiliative interactions might be beneficial for both
109 males and females. These kinds of sex-biased interactions might additionally depend on age
110 differences between siblings (Lonsdorf et al., 2018). Lastly, for females in particular, sororal

111 relationships may exert important influences on future rank and resource acquisition outcomes
112 (Charpentier et al., 2008; Lea et al., 2014; cf. Engh et al., 2009).

113 Addressing the issues reviewed above, and understanding the nature and evolution of
114 cooperative social relationships in primates more generally, requires long-term investigations of
115 species that reveal how individuals respond behaviorally to socioecological variation (e.g. Albers &
116 Altmann, 2012). With this principle in mind, mountain gorillas in particular are a compelling
117 comparative model for the evolution and development of human sibling relationships. Long-term
118 monitoring of wild mountain gorillas by the Dian Fossey Gorilla Fund has revealed social structures
119 marked by extensive diversity in relatedness, age proximity, and sex makeup infrequently observed in
120 other primate groups (Robbins et al., 2009; Roy et al., 2014). Mountain gorillas regularly form multi-
121 female, single-male groups, as well as multi-female, multi-male groups in which multiple males
122 reproduce, though paternity data and unsophisticated paternal kin discrimination mechanisms are
123 consistent with historically high reproductive skew (Bradley et al., 2005; Rosenbaum et al., 2015;
124 Vigilant et al., 2015). As a result of this structure, co-resident offspring have a reasonable chance of
125 being full siblings, paternal half-siblings, maternal half-siblings, or unrelated to one another. Like
126 humans, both males and females, upon reaching maturity, may opt to disperse or remain in their
127 natal groups (Robbins et al., 2009; Stoinski et al., 2009), which permits fraternal, sororal, and mixed-
128 sex relationships that can last for an entire lifespan.

129 In the present study, we use nearly 40,000 hours of behavioral data spanning 14 years to
130 describe patterns of interactions between siblings and demographically-comparable non-sibling
131 dyads in social groups of wild mountain gorillas. Using extensive maternity and genetic paternity
132 data available for 157 identifiable individuals, we examine whether full siblings, maternal half-
133 siblings, paternal half-siblings, and unrelated co-residents exhibit differing patterns of affiliation

134 (playing, grooming, and time spent in close proximity) and agonism (contact and non-contact
135 aggression) in line with models of kin selection, after adjusting for the potential mediating presence
136 of mothers in these interactions. Evidence of relatively weak kin discrimination among gorilla
137 fathers and offspring (Rosenbaum et al., 2015, though see also Vigilant et al., 2015 for evidence of
138 father-daughter inbreeding avoidance) might suggest correspondingly weak social bias toward
139 paternal half-siblings, along with strong bias toward full siblings and maternal half-siblings; we test
140 this speculation for the first time in this species. We also investigate whether familiarity, as indexed
141 by age differences between social partners, predict patterns of affiliative or agonistic behavior, and
142 whether these patterns differ between kin categories—particularly paternal and maternal kin (as some
143 evidence from cercopithecine monkeys suggests; e.g. Widdig et al., 2002).

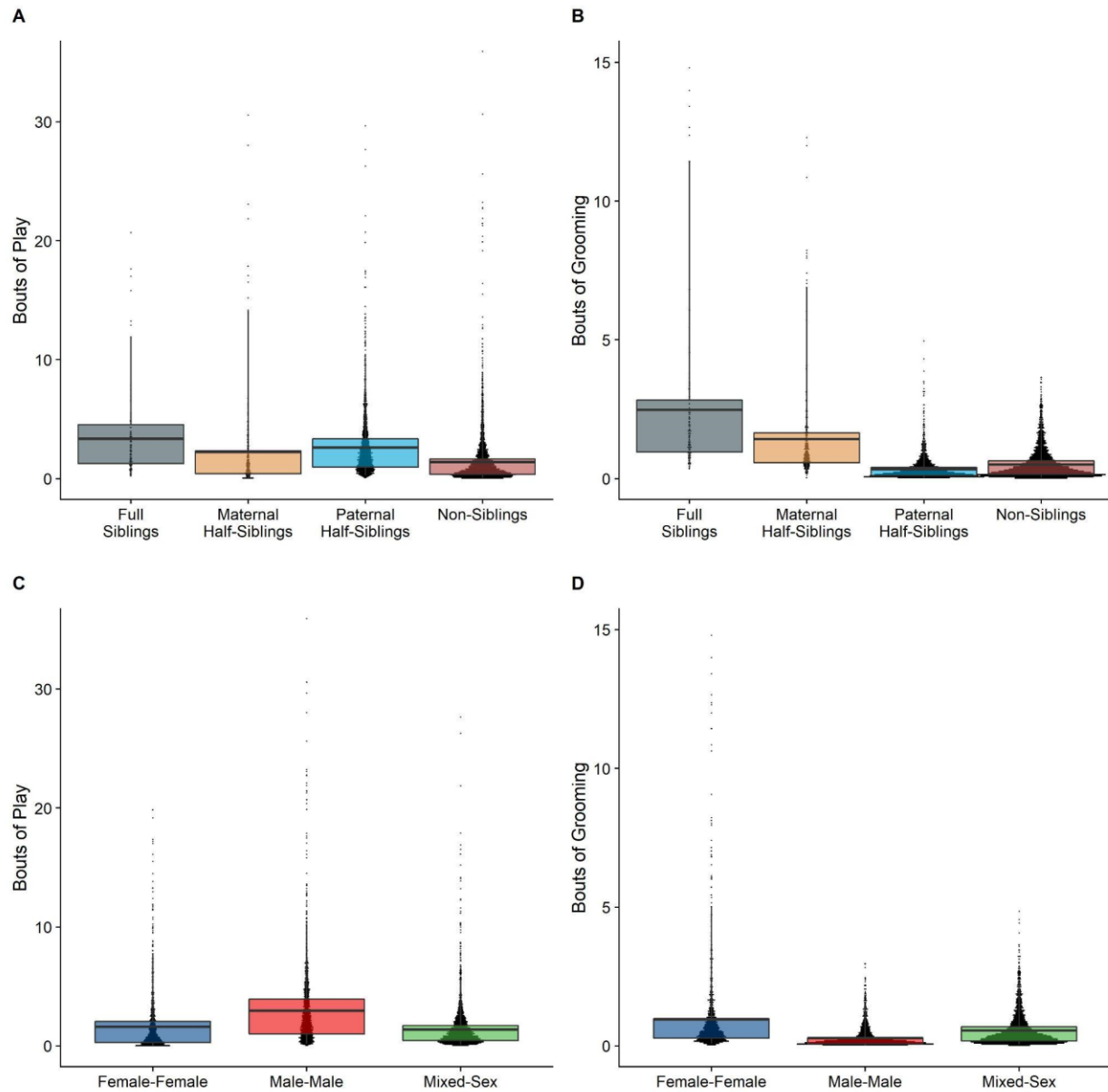
144 Lastly, we explore sex makeup as a third axis of variation potentially relevant for
145 understanding sibling and co-resident social relationships. We test whether male-male, female-
146 female, and mixed-sex sibling relationships are characterized by differing rates and types of social
147 interactions, and whether these sex category differences are restricted to kin. Via these comparisons,
148 we ask whether differences are consistent with the kinds of benefits siblings might be expected to
149 deliver later in life: for example, among males, are fraternal relationships marked by higher rates of
150 playing and fighting, and sororal relationships higher rates of grooming?; among females, are sororal
151 relationships marked by the highest rates of grooming compared to any other dyad configuration?;
152 are affiliative patterns unique to siblings, or are comparable trends found in unrelated dyads?

153 **Results**

154 *Affiliative Behaviors.* In our full sample of 1957 unique dyads spanning 7,858 dyad-years, full
155 siblings (n=43 dyads) played and groomed each other significantly more than did paternal siblings
156 (n=555 dyads) or non-siblings (n=1258 dyads; all comparisons $p < 0.001$; Figure 1A, 1B). Maternal

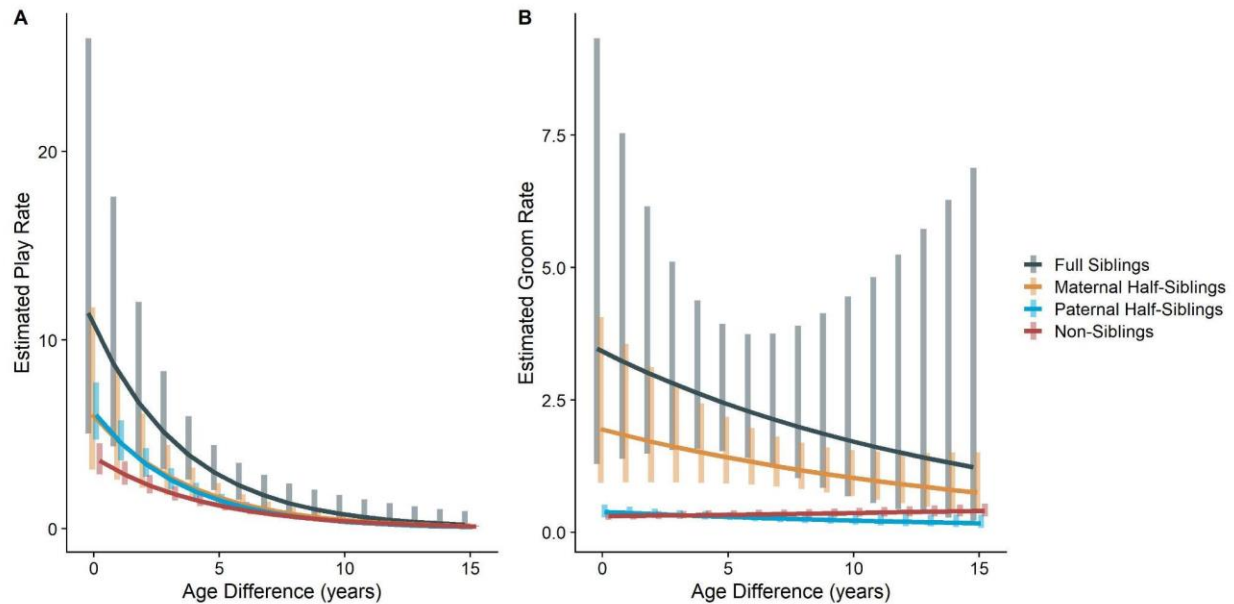
157 siblings (n=101 dyads) played significantly less than full siblings, but groomed at comparable rates.
158 Age differences (in our sample, mean: 5.90 years; SD: 4.57 years; range: 0 – 23.5 years) interacted
159 with relatedness in predicting grooming ($p = 0.023$), but not play ($p = 0.076$). Play consistently
160 dropped for siblings and non-siblings alike as age differences increased (γ ranging from -0.23 – -0.28,
161 all $p < 0.001$; Figure 2A). By contrast, grooming rates were relatively unrelated to age differences
162 between partners (γ ranging from -0.07 – 0.02, all $p > 0.05$; Figure 2B).

163 **Figure 1. Box and dot plots comparing relatedness categories (A, B) and sex**
164 **categories (C, D) for play rates (left) and grooming rates (right).**



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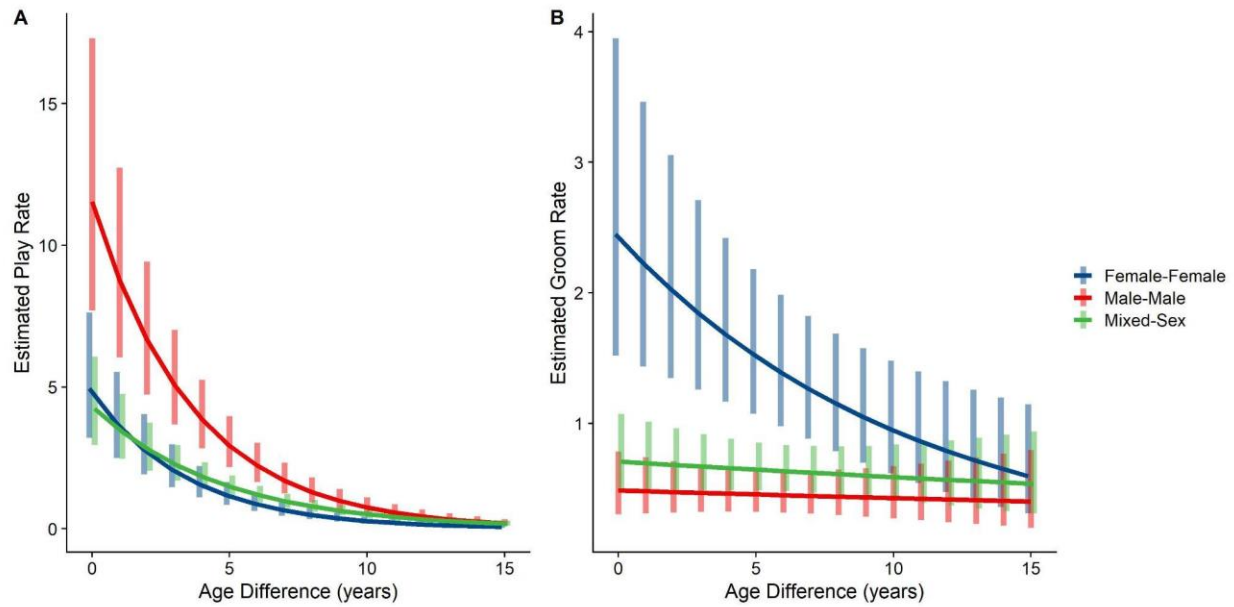
166 **Figure 2. Estimated rates of play (A) and grooming (B) across a range of age differences,**
167 **separated by relatedness category. Bars represent 95% confidence intervals for rates of**
168 **behavior at a given age difference.**



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170 Male-male dyads ($n=520$) played more than either mixed-sex ($n=981$) or female-female
171 dyads ($n=456$); conversely, female-female dyads groomed each other more than either mixed-sex or
172 male-male dyads (all $p < 0.001$; Figure 1C, 1D). These patterns too were significantly moderated by
173 age differences ($p < 0.002$), but not relatedness ($p = 0.078$ and 0.112). Play dropped rapidly with
174 increasing age differences ($\gamma = -0.29 - -0.21$) for all sex configurations (all $p < 0.001$; Figure 3A).
175 Grooming was steadily low in male-male and mixed-sex dyads ($\gamma = -0.01$ and -0.02 , $p > 0.45$),
176 though it dropped with increasing age differences in female-female dyads ($\gamma = -0.09$, $p = 0.001$),
177 such that differences between sex categories became indistinguishable after approximately a 10-year
178 age difference (Figure 3B).

179 **Figure 3. Estimated rates of play (A) and grooming (B) across a range of age differences,**
180 **separated by sex category. Bars represent 95% confidence intervals for rates of behavior at a**
181 **given age difference.**



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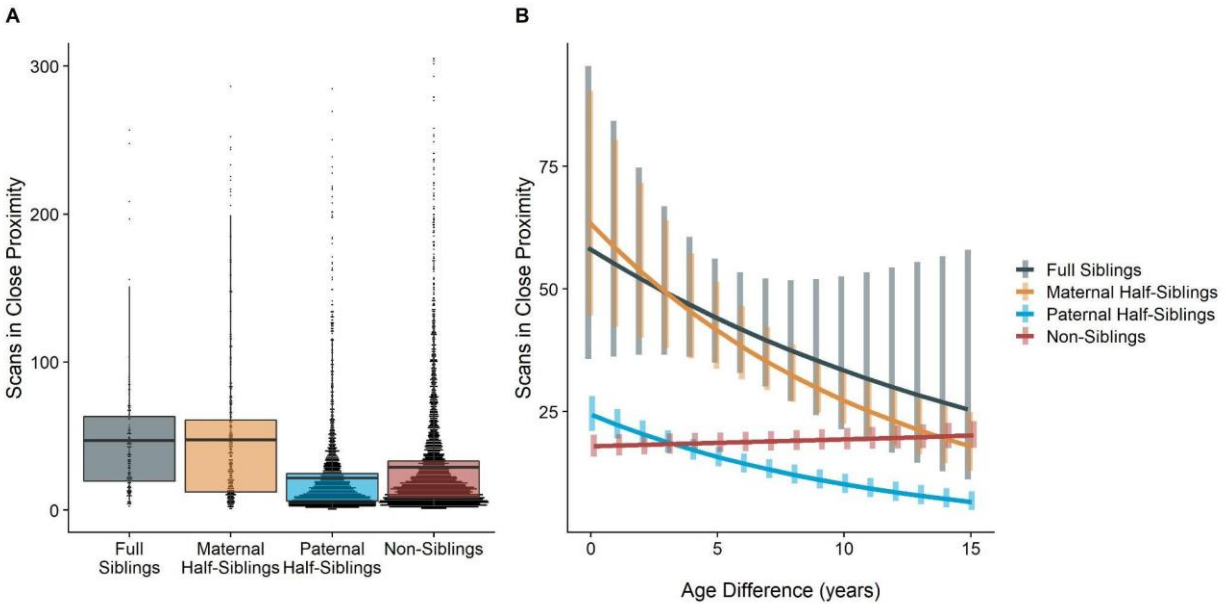
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Time spent in proximity. The time dyads spent in close proximity (<2 m) with each other also varied between relatedness categories ($p < 0.001$), with maternal siblings and full siblings once again spending more time near each other than non-siblings, who themselves spent more time in close proximity than paternal siblings did (all comparisons $p < 0.001$; Figure 4A). However, these patterns too were moderated by age differences ($p < 0.001$). Proximity decreased with increasing age differences in maternal siblings and paternal siblings ($\gamma = -0.08$ and -0.09 , $p < 0.001$), but did not decrease significantly in full siblings or non-siblings ($\gamma = -0.06$ and 0.01 , $p > 0.19$). Thus, while all classes of siblings spent more time near each other than non-siblings when near in age, even when adjusting for their mother's presence, this distinction was partially reversed at large age differences, when paternal siblings spent much less time near each other than any other dyad category (Figure 4B).

195 **Figure 4. Box and dot plots (A) and estimated trends across a range of age differences (B)**
196 **for the time gorilla dyads spent in close proximity, separated by relatedness category. Bars**
197 **in (B) represent 95% confidence intervals for rates of proximity at a given age difference.**

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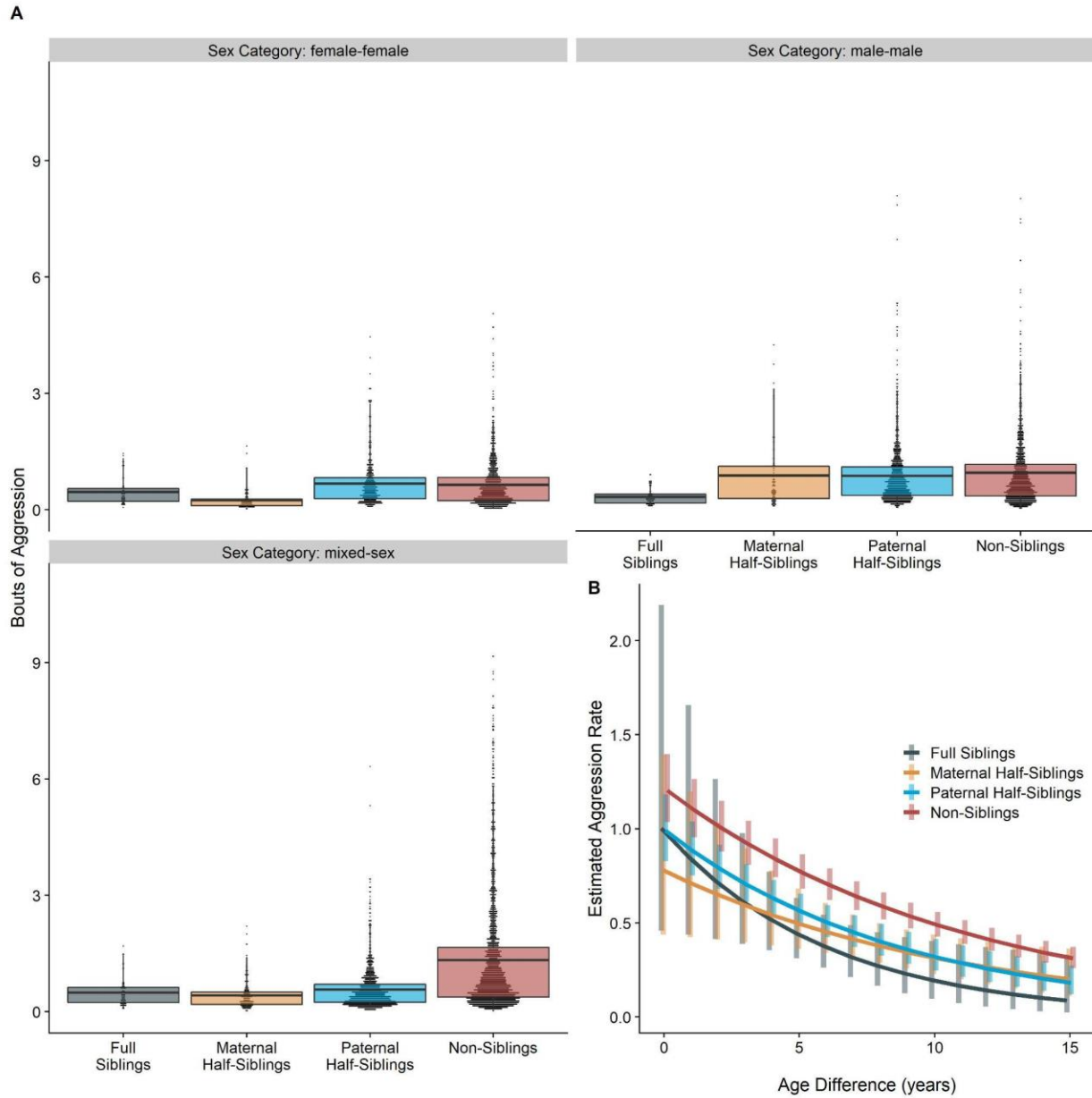


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200 *Competitive Behaviors.* Neither relatedness nor sex category on their own significantly predicted
201 rates of aggressive behavior ($p = 0.205$ and 0.763 , respectively). However, our model did reveal a
202 significant sex makeup \times relatedness interaction term ($p = 0.049$; Figure 5A). Decomposing this
203 interaction, among female-female and male-male dyads, there were no statistically significant
204 contrasts between relatedness categories. In mixed-sex dyads, non-siblings engaged in substantially
205 more aggression than any sibling category (all $p < 0.031$).

206 Dyads more distant in age engaged in less aggression than dyads that were closer in age,
207 regardless of relatedness or sex makeup ($\beta = -2.11$, $p = 0.035$; Figure 5B).

208 **Figure 5. Box and dot plots (A) and estimated trends across a range of age differences (B)**
209 **for aggression within gorilla dyads, separated by relatedness and sex category. Bars in (B)**
210 **represent 95% confidence intervals for rates of aggression at a given age difference.**



211

212 **Discussion**

213 In a comprehensive examination of dyadic mountain gorilla social relationships spanning 14
214 years and nearly 40,000 hours of observation, we find complex patterns of affiliation and
215 competition within gorilla pairs that speak to sex-, age-, and relatedness-specific social biases. In
216 general, siblings affiliated with each other more and spent more time together than non-siblings,
217 even when accounting for the presence of mothers. But within siblings, affiliative patterns further
218 varied: full and maternal siblings were in most cases much more affiliative than paternal siblings,
219 whose behavior more closely resembled that of non-siblings. We consistently observed a trend for
220 male-male dyads to play more, for female-female dyads to groom more, and for mixed-sex dyads to
221 fall intermediate between these groups. Examining competitive behaviors, on the other hand,
222 revealed a more narrow sibling bias. Aggression was most common in mixed-sex non-sibling dyads,
223 and larger age differences similarly predicted less aggression across all dyad types.

224 At the broadest level, our results support the existence of affiliative biases towards kin in
225 mountain gorillas. While past research has been largely equivocal about the extent of kin
226 discrimination that relies on mechanisms beyond familiarity (Wikberg et al., 2014; Godoy et al.,
227 2016; Lynch et al., 2017)—and indeed, our results do support a role of familiarity in structuring social
228 interactions—our findings are unlikely to be entirely explained by mere exposure for at least three
229 reasons:

230 First, gorilla social groups are tight-knit and cohesive compared to their close ape relatives
231 (Goodall, 1986; Remis, 1997; Morrison et al., 2021), such that all individuals in a group, related or
232 not, are very likely quite familiar with one another. Second, our results pertaining to prosocial biases
233 towards siblings are not fully explained by familiarity or exposure, as indexed by age differences
234 (Widdig et al., 2001; Smith et al., 2003; Lynch et al., 2017). We observed clear biases towards kin at
235 all but the largest age differences—and some siblings in our data set were 20 or more years apart in

236 age—even though sibling and non-sibling age-mates in the same social group would typically be
237 expected to possess close familiarity. Finally, while mothers undoubtedly mediate social interactions
238 of offspring, especially for immature individuals, biases towards siblings persist even when adjusting
239 for the frequency of her presence during interaction periods. Jointly, these considerations suggest a
240 sibling bias in mountain gorillas subject to influence, but not determination, by demographic factors,
241 which we interpret as aiding in the development of sibling relationships that exist across timescales
242 rarely observed in other non-human primates.

243 The observation that full and maternal siblings groomed, played, and spent more time near
244 each other than paternal siblings or non-siblings, who tended to affiliate at comparable rates, further
245 suggests that mountain gorillas, like several other primate species studied (Langergraber et al., 2007;
246 Silk et al., 2006; Lynch et al., 2017), evince much stronger maternal than paternal kin bias (see also
247 Rosenbaum et al., 2015, which found little evidence for paternal kin discrimination among fathers
248 and offspring). Interestingly, this “asymmetric bias” in affiliation seems to persist despite mountain
249 gorillas lacking a key element of the social structure hypothesized to underlie it in other species:
250 namely, low reproductive skew (Galezo et al., 2022). Thus, one question concerns why mountain
251 gorillas do not appear to more strongly favor paternal siblings. Current evidence indicates that
252 single-male gorilla groups across research sites are entirely genetically polygynous (reviewed in
253 Rosenbaum & Silk, 2022), and while there can be considerable temporal variation, reproductive
254 skew is generally much higher in multi-male gorilla groups than in, for example, chimpanzee,
255 savannah baboon, or rhesus macaque groups (Vigilant et al. 2015, Surbeck et al. 2017, Alberts et al.
256 2003, Widdig et al. 2004). We propose that, despite possessing a mating system quite unlike these
257 other primate species, mountain gorillas still exhibit a comparable maternal sibling bias due to a
258 mismatch between their historical mating structure—which we speculate consisted of highly
259 polygynous one-male units—and their contemporary social structure of tight-knit, often multi-male

260 groups. In other words, while individuals in highly polygynandrous groups might find it too
261 difficult to detect and adjust affiliation toward paternal kin, perhaps mountain gorillas fail to do so
262 because, until very recently, it was unnecessary. If co-residency was enough to identify paternal kin
263 with reasonable accuracy, a more sophisticated recognition mechanism would be unlikely to evolve.

264 Notably, while we see little evidence that mountain gorillas show a prosocial bias towards
265 paternal siblings, patterns of aggressive behavior suggest there may still be kin recognition
266 mechanisms at play for all sibling types. Aggression remained low across most combinations of
267 relatedness and sex configurations, with one exception: mixed-sex interactions among non-siblings.
268 This pattern is consistent with males deploying aggression in the context of mate attraction or
269 coercion. Past research in gorillas suggests male aggression towards females may have a number of
270 non-mutually exclusive functions within those domains: to police female-female aggression, to
271 discourage female dispersal or mate choice, or to indicate protective ability or overall condition
272 (Robbins, 2009; Breuer et al., 2016). The fact that this kind of aggression was observed less
273 frequently among related male-female pairs is another observation consistent with accurate kin
274 discrimination. It also suggests active inbreeding avoidance, to the extent that aggression truly serves
275 a mate attraction function. While death and dispersal have been suggested to obviate the need for
276 sophisticated inbreeding avoidance mechanisms in some primates (e.g. baboons; Galezo et al., 2022),
277 such an explanation is unlikely to apply to contemporary mountain gorillas. Living with opposite-sex
278 relatives after sexual maturity is a routine occurrence in this species. Prior research confirms strong
279 inbreeding avoidance between father-daughter dyads in this species (Vigilant et al. 2015), but further
280 work is needed to investigate the extent to which male mate choice is manifested via female-directed
281 aggression, and whether females, for their part, possess additional mechanisms to avoid mating with
282 kin, including paternal siblings.

283 Together, these observations—prosocial biases towards kin that do not appear to be fully
284 explained by familiarity; a stronger maternal than paternal sibling prosocial bias; and avoidance of
285 intersexual aggression across all sibling types—both speak to key questions about the development of
286 great ape sibling relationships and present two additional puzzles for interpretation. First, traditional
287 mechanistic explanations for sibling biases that typically appeal to exposure during developmental
288 periods appear largely inconsistent with our results and the nature of mountain gorilla sociality, in
289 which siblings and non-siblings, and maternal and paternal siblings, are all likely to have significant
290 exposure to one another during development. It is possible that early-life exposure effects via
291 repeatedly sharing night nests (Fossey, 1979) function analogously to the manner in which co-
292 residence duration serves as a key component of kin recognition in humans (Lieberman et al., 2007),
293 or that preferential mother-father relationships post-birth might lead to social preferences among
294 siblings (Rosenbaum et al., 2016). Individuals may also possess some degree of phenotype matching
295 ability (Widdig, 2007; Parr et al., 2010; Langergraber, 2012; Pfefferle et al., 2014).

296 Second, the lack of evidence for a prosocial bias towards paternal siblings is not readily
297 reconciled with clear behavioral evidence of reduced aggression within these same dyads. This
298 remarkable disjunct between apparent sibling recognition and sibling bias suggests that from a
299 mountain gorilla’s perspective, paternal siblings are known entities that nevertheless are less
300 attractive social partners than maternal siblings, despite each being equal relatives. There may be
301 multiple, non-mutually exclusive explanations for this dynamic. Perhaps the presence of paternal
302 siblings provides fewer benefits to an individual than do other sibling types—this possibility, while
303 previously suggested (e.g. Cords et al., 2018), has not been systematically investigated and is an ideal
304 target for future research. A mismatch between historical and current social structure might also lead
305 to inconsistent, weakened kin recognition among paternal siblings that manifests in the contrasting
306 patterns we report. Ultimately, disentangling these potential explanations within a species that only

307 exists in the wild may depend on the opportunity to study long-term mating patterns and the
308 impacts of “natural experiments” such as early maternal loss or adoption (most often carried out by
309 adult males in this species; Fossey, 1979, Morrison et al. 2021).

310 **Conclusion**

311 Our analyses of sibling relationships in mountain gorillas provide extensive, large-scale
312 information on the dynamics of cooperation and competition in a primate society where, as in
313 humans, potential social partners vary greatly in the genes, developmental stage, and biological sex
314 they share with each other. We find a selective sibling bias for prosocial behaviors, in that siblings
315 who share matrilineal kinship affiliate at greater rates than either paternal half-siblings or non-
316 siblings, and that this bias weakens as individuals become more distant in age. While such a result is
317 consistent with a wide range of previous research, none of the reasons proposed for this selective
318 bias in primates appear to apply to our population: mountain gorillas gain regular exposure to
319 siblings of all types, across their entire lives; furthermore, patterns of aggressive behavior, in contrast
320 to affiliation, suggest that mountain gorillas can in fact recognize paternal siblings, though they
321 evidently do not favor them as cooperative partners. Ultimately, our study underscores a diversity of
322 means, some evidently yet to be revealed, through which individuals might perceive and engage in
323 sibling relationships to achieve fitness outcomes.

324 **Materials and Methods**

325 Our study subjects came from a population of habituated wild mountain gorillas living in
326 Volcanoes National Park, Rwanda, that have been monitored nearly continuously for the last 54
327 years by the Dian Fossey Gorilla Fund. Using focal follow and scan data collected by researchers
328 and staff, we compiled a dataset of all available dyadic gorilla behavior spanning the years of 2003 to
329 2017. We then supplemented this dataset with demographic and relatedness data (for maternal

330 relatedness, via direct observation; for paternal relatedness, via genetic paternity determination—see
331 e.g. Vigilant et al., 2015) on individuals pulled from long-term records. From this combined dataset,
332 we excluded interactions with infants <1 year of age at time of observation, parent-offspring
333 interactions, and interactions between dyads for which we could not calculate relatedness from
334 available data. This yielded a final, curated dataset containing 157 unique individuals (75F, 82M;
335 average age at time of observation = 9.75 years) and 38,996 total hours of observation.

336 *Composition of dyads.* Our dataset of behavior from 157 individuals contained 1957 unique
337 dyad pairs. Of these dyads, 1258 shared neither a mother nor father (“non-siblings”), 555 shared a
338 father but not a mother (“paternal siblings”), and 43 shared both a mother and a father (“full
339 siblings”). In addition to dyads known to share a mother but not a father (n = 50), there were a
340 number of dyads with the same mother, but with paternity data missing for one or both individuals
341 (n = 51). To maximize sample size, we combined these two groups into the category of “maternal
342 siblings”; due to this analytic choice, this category can be effectively conceived of as “at least
343 maternal siblings”. See Tables S1 and S2 in Supplementary Materials for analyses using only
344 confirmed maternal siblings, which were very similar to those reported below. Mixed-sex dyads were
345 the most common sex category in our dataset (n = 981), followed by male-male (n = 520) and
346 female-female (n = 456). Dyads differed in age by an average of 5.90 years (SD: 4.57 years; range: 0
347 – 23.5 years); for reference, the average interbirth interval in mountain gorillas is 3.9 years (Eckardt
348 et al., 2016). We used this age difference variable as our primary index of familiarity between
349 individuals. While we also had information on the natal groups of individuals, which could also serve
350 as a potential index of familiarity, we do not focus on this variable in analyses, as it did not allow us
351 to disambiguate between relatedness and familiarity—dyads of individuals who grew up in different
352 natal groups were virtually never (n = 3) siblings in our dataset.

353 *Behavioral Measures.* We evaluated five different categories of dyadic behaviors as outcome
354 variables: grooming, playing, non-contact aggression, contact aggression, and time spent in close
355 (2m) proximity. We operationalized these behaviors from standardized definitions used in previous
356 publications about this gorilla population (see e.g. Rosenbaum et al., 2015). Trained observers
357 regularly undergo interobserver reliability tests. The former four behavioral categories were
358 evaluated as counts (corrected for exposure time; see *Data Analysis*) within the dyad during focal
359 observations, regardless of directionality, while the latter category of time in close proximity was
360 evaluated by counting the number of instantaneous scan samples in which a dyad was observed
361 within 2 m of each other (also corrected for exposure time).

362 *Data Analysis.* We conducted all analyses in R (version 4.1.2). Our main statistical models for
363 each behavioral outcome consisted of cross-classified generalized linear mixed models (conducted
364 using the *glmmTMB* package; Brooks et al., 2017) that included random intercepts for each individual
365 within the dyad, as well as the dyad itself. Given low incidences of many behaviors, we aggregated
366 behaviors into annual counts, making the dyad-year the fundamental unit of analysis (total n =
367 7858). Even with annual aggregation, instances of aggression were uncommon. Therefore, counts of
368 contact and non-contact aggression were summed into a single category for analysis (see Tables S3
369 and S4 and Figures S1 and S2 in Supplementary Materials for results with individual aggression
370 categories, which were qualitatively similar to those reported below).

371 In models predicting each behavioral outcome, we included terms for relatedness, age
372 difference, and sex makeup, as well as two-way interactions between relatedness and sex makeup,
373 relatedness and age difference, and sex makeup and age difference. As mothers plausibly mediate
374 many of the social behaviors we examined, especially early in life, we also included the average
375 proportion of observations with mothers in close proximity, and this variable's interaction with

376 relatedness, as covariates in all models. In models containing significant main effect or interaction
377 terms, we decompose omnibus comparisons and report targeted marginal effects and contrasts using
378 the *emmeans* package (Lenth, 2022), with all reported *p*-values corrected for false discovery rate. We
379 modeled our count outcomes as rates with a negative binomial family in *glmmTMB* and offset term
380 for exposure time (either logged hours of observation, or logged sum of scans for both individuals,
381 per dyad-year). For each model, we verified model fit by inspecting the deviation, dispersion, and
382 outliers of residuals using the *DHARMa* package (Hartig, 2022). All data and code necessary to
383 reproduce our results are available publicly at <https://osf.io/6qgj5>.

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393 **Competing Interests**

394 The authors report no competing interests.

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400 **References**

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Supplementary Analyses for “Neither kin selection nor familiarity explain affiliative biases towards maternal siblings in wild mountain gorillas”

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Tables S1 – S2. Results for analyses using a ‘stricter’ categorization of maternal siblings (n = 50; see Methods for details of categorization; total dyad-years: 7625).

Table S1. Omnibus statistics for target parameters (full model results available from data and code posted publicly at <https://osf.io/6qgj5>). Effects $p < 0.05$ bolded.

	Effect					
	Relatedness	Sex Category	Age Differences	Rel. × Sex Category	Rel. × Age Diff.	Sex × Age Diff.
Play	$\chi^2(3) = 16.58$, $p < 0.001$	$\chi^2(2) = 13.64$, $p = 0.001$	$\chi^2(1) = 15.51$, $p < 0.001$	$\chi^2(6) = 8.06$, $p = 0.234$	$\chi^2(3) = 7.05$, $p = 0.070$	$\chi^2(2) = 16.83$, $p < 0.001$
Grooming	$\chi^2(3) = 16.05$, $p < 0.001$	$\chi^2(2) = 10.88$, $p = 0.004$	$\chi^2(1) = 2.08$, $p = 0.149$	$\chi^2(6) = 6.88$, $p = 0.331$	$\chi^2(3) = 8.44$, $p = 0.038$	$\chi^2(2) = 13.94$, $p < 0.001$
Proximity	$\chi^2(3) = 17.64$, $p < 0.001$	$\chi^2(2) = 1.69$, $p = 0.423$	$\chi^2(1) = 1.58$, $p = 0.209$	$\chi^2(6) = 7.74$, $p = 0.258$	$\chi^2(3) = 63.81$, $p < 0.001$	$\chi^2(2) = 0.30$, $p = 0.985$
Aggression	$\chi^2(3) = 1.46$, $p = 0.691$	$\chi^2(2) = 0.54$, $p = 0.762$	$\chi^2(1) = 4.30$, $p = 0.022$	$\chi^2(6) = 11.52$, $p = 0.073$	$\chi^2(3) = 2.68$, $p = 0.443$	$\chi^2(2) = 6.67$, $p = 0.036$

Table S2. Estimated marginal means and standard errors across relatedness and sex categories.

	Relatedness				Sex Category		
	Full Siblings	Maternal Half	Paternal Half	Non-Siblings	Female - Female	Male - Male	Mixed - Sex
Play	2.91 (0.58)	1.83 (0.42)	1.42 (0.17)	1.14 (0.11)	1.17 (0.22)	2.95 (0.50)	1.46 (0.20)
Grooming	2.51 (0.60)	1.61 (0.45)	0.30 (0.04)	0.34 (0.04)	1.49 (0.30)	0.48 (0.10)	0.73 (0.11)
Proximity	44.9 (5.5)	42.6 (5.9)	15.8 (1.0)	18.9 (1.0)	30.2 (3.2)	25.9 (2.6)	26.4 (2.1)
Aggression	0.43 (0.08)	0.64 (0.13)	0.56 (0.04)	0.76 (0.05)	0.50 (0.07)	0.68 (0.09)	0.60 (0.06)

Tables S3 – S4, Figures S1-S2. Results for analyses assessing contact aggression and non-contact aggression separately (total dyad-years: 7822).

Table S3. Omnibus statistics for target parameters (full model results available from data and code posted publicly at <https://osf.io/6qgj5>).

	Effect					
	Relatedness	Sex Category	Age Differences	Rel. × Sex Category	Rel. × Age Diff.	Sex × Age Diff.
Contact Aggression	$\chi^2(3) = 5.58,$ $p = 0.134$	$\chi^2(2) = 1.57,$ $p = 0.456$	$\chi^2(1) = 1.48,$ $p = 0.223$	$\chi^2(6) = 10.54,$ $p = 0.104$	$\chi^2(3) = 0.34,$ $p = 0.953$	$\chi^2(2) = 3.74,$ $p = 0.154$
Non-Contact Aggression	$\chi^2(3) = 2.96,$ $p = 0.398$	$\chi^2(2) = 3.35,$ $p = 0.187$	$\chi^2(1) = 1.92,$ $p = 0.166$	$\chi^2(6) = 10.23,$ $p = 0.116$	$\chi^2(3) = 1.17,$ $p = 0.760$	$\chi^2(2) = 2.22,$ $p = 0.330$

Table S4. Estimated marginal means and standard errors across relatedness and sex categories.

	Relatedness				Sex Category		
	Full Siblings	Maternal Half	Paternal Half	Non-Siblings	Female - Female	Male - Male	Mixed - Sex
Contact Aggression	0.23 (0.04)	0.22 (0.04)	0.28 (0.02)	0.34 (0.02)	0.22 (0.03)	0.28 (0.04)	0.30 (0.03)
Non-Contact Aggression	0.10 (0.03)	0.18 (0.04)	0.18 (0.02)	0.23 (0.02)	0.18 (0.03)	0.18 (0.03)	0.13 (0.02)

Figure S1. Box and dot plots showing estimated non-contact aggression within gorilla dyads, separated by relatedness and sex category.

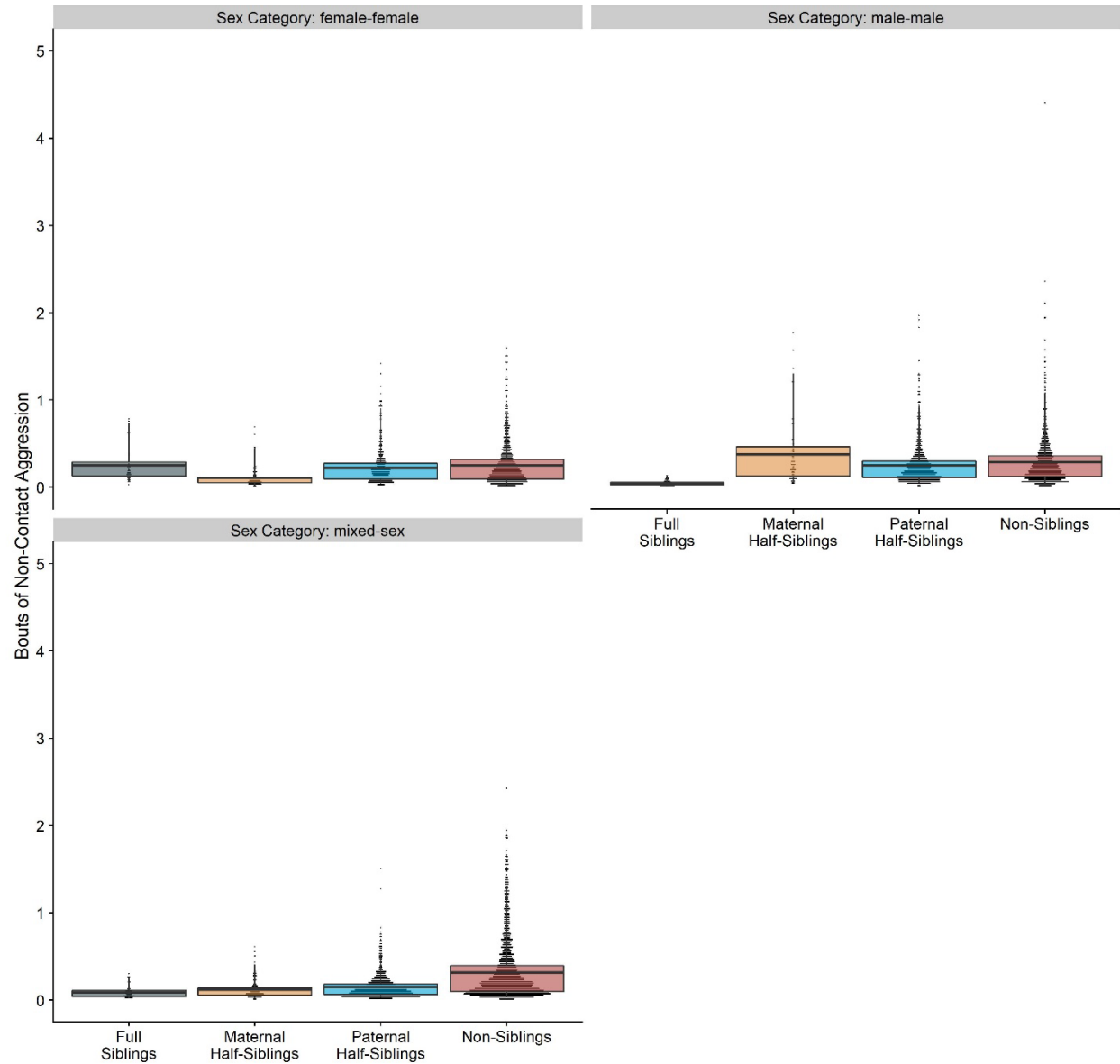


Figure S2. Box and dot plots showing estimated contact aggression within gorilla dyads, separated by relatedness and sex category.

