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Paternal kin discrimination by sons in male chimpanzees transitioning to adulthood

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28 **Abstract**

29

30 Although paternal investment explains the evolution of fatherhood from a functional perspective,
31 its evolutionary origins are unclear. Here we investigate whether a building block for paternal
32 investment, father-offspring discrimination, is present in our closest living relatives,
33 chimpanzees. Adolescent and young adult males (12 - 21 years old) maintained proximity and
34 groomed with their fathers more frequently than with other males given how often they
35 associated. This discrimination did not likely increase the short-term inclusive fitness of fathers
36 or sons because the absolute time they spent in proximity or grooming did not exceed the time
37 spent in these activities by other dyads. Almost all grooming was done by sons rather than
38 fathers, suggesting that sons are responsible for observed biases in father-son behavior. Father-
39 offspring discrimination could partly be explained by young males socializing with males who
40 were more likely to be their father based on their age at the time of the young male's conception.
41 Two other cues of paternity, the other male's rank at the time of the young male's infancy and
42 the other male's association frequency with the young male's mother during the young male's
43 infancy/juvenility, failed to predict association-controlled proximity or grooming. Father-son
44 biases persisted even after controlling for characteristics of males that predicted paternity
45 probability, implicating other cues that we did not examine. These results suggest that an
46 important factor for the evolution of highly investing fathers in humans, father-offspring
47 discrimination, may have been present in simpler form in the last common ancestor they shared
48 with chimpanzees.

49

50

51 **Introduction**

52

53 In most human societies, fathers contribute to the health and fitness of their offspring.
54 Through co-evolution with sexual-division of labor, this has led to the unusual combination of
55 high fertility and low mortality responsible for our ecological dominance of the planet (1-6).
56 Although human fatherhood has been well studied from this functional perspective, its evolution
57 (sensu 7) remains puzzling. Phylogenetic inertia plays a strong role in the evolution of social and
58 mating systems, with those of closely related species generally being very similar (8, 9). Yet in
59 humans' closest living relatives, chimpanzees and bonobos, females are highly promiscuous and
60 mate with many adult males during each conception cycle (10-12). Like all complex adaptations,
61 human fatherhood represents the end-product of a multi-step evolutionary sequence in which
62 more elaborate forms succeeded one another (13). For fathers to invest heavily in their offspring,
63 they must first evolve a capacity for kin discrimination, which refers to differences in behavioral
64 responses individuals show toward kin compared to non-kin using conspecific cues correlated
65 with kinship (14).

66 Pair bonds play a key role in father-offspring discrimination in all contemporary human
67 societies. In these, fathers discriminate their offspring born by the woman with whom they had a
68 pair-bond and more or less exclusive sexual access, and offspring discriminate their father as the
69 man who had a long-term pair-bond with their mother (13, 15, 16). Although highly investing
70 fathers seem to occur only in species with strong pair-bonds (e.g., titi monkeys: 17), a growing
71 body of evidence shows that weaker father-offspring discrimination occurs in species where
72 females mate promiscuously (18-24). This evidence includes two studies of chimpanzees
73 suggesting that fathers show slight tendencies to play and groom with their own infants and
74 juveniles (25, 26).

75 Several non-mutually exclusive cues can contribute to father/offspring discrimination in
76 promiscuous species. Some cues are indirect and rely on the fact that even in the most
77 promiscuous species paternity success is not entirely random but instead is correlated with
78 certain male characteristics (14, 27, 28). For example, in the Ngogo community of chimpanzees,
79 the probability that a male is the father of an offspring is predicted by his dominance rank at the
80 time of conception and his long-term tendency to associate with the offspring's mother (29).
81 Biases in the social behavior between chimpanzee offspring and fathers could thus arise as a
82 byproduct of offspring preferentially interacting with males who were high ranking and
83 frequently associated with their mothers when offspring were young. Alternatively, a similar bias
84 would result if fathers preferentially interact with offspring born to females with whom they
85 frequently associated when they were high ranking. Baboons provide some of the strongest
86 evidence for father-offspring discrimination in promiscuously mating mammals as females form
87 special relationships with formerly high-ranking males who are likely to be the fathers of their
88 offspring (18, 21, 30, 31).

89 Age is another indirect cue for paternal kin recognition in promiscuous species. In several
90 female-philopatric primate species, adult females similar in age tend to socialize. These
91 individuals are likely to be paternal sisters because only a small number of males reproduce at
92 any given time (32-34). However, unlike paternal siblings, fathers and offspring are by necessity
93 very different rather than similar in age, as paternity success typically has an inverted-U
94 relationship with age, increasing from sexual maturity, peaking in prime adulthood, and
95 declining thereafter (35). Whether animals use differences in age as a cue of a father-offspring
96 relationship is unknown.

97 Father-offspring discrimination may also involve direct cues (sensu 14, 27) as occurs in
98 phenotype matching, where individuals discriminate among conspecifics based on their
99 perceived phenotypic and thus genetic similarity to themselves or known kin. Evidence for
100 phenotype matching has been demonstrated experimentally (36, 37), but more often is invoked
101 when other indirect cues have been excluded, especially in field studies of animals in the wild
102 (28, 38).

103 In this paper, we investigate father-offspring discrimination and its underlying cues in wild
104 chimpanzees. Unlike previous research on kin discrimination in promiscuous species, which
105 focused on behavior between fathers and sexually immature offspring (i.e., infants and
106 juveniles), we examine behavior between fathers and sexually mature offspring (i.e., adolescents
107 and young adults). We focus on male offspring because they remain in their natal community,
108 and thus unlike females who disperse, have opportunities to socialize with their fathers well past
109 sexual maturity. Opportunities for sexually mature males to interact with their fathers are
110 especially likely in our particular chimpanzee study group at Ngogo in Kibale National Park,
111 Uganda, where minimal human disturbance and an abundant food supply support an unusually
112 large community (N = 193 individuals), whose individuals survive at high rates and live a long
113 time (39).

114 During 12 months we recorded the amount of time 18 adolescent and young adult males
115 ('young males,' age range: 12-21 years) spent with one another and with 36 other younger
116 adolescent and older adult males (8 - 53 years, including 11 fathers) in: (1) association in the
117 same party; (2) spatial proximity of ≤ 5 m; and (3) grooming. While proximity and grooming are
118 widely considered to be meaningful measures of affiliative social behavior in non-human
119 primates, their analysis is complicated in fission-fusion species like chimpanzees, where dyads

120 vary in their opportunities to perform these behaviors based on how often they associate in
121 temporary subgroups or ‘parties’ (40). Association, in turn, reflects social preferences, but also
122 additional social, ecological, and other constraints (41). We compare levels of proximity and
123 grooming in father-son and other types of dyads with and without controls for frequency of
124 association, interpreting the former as an indication of discrimination and the latter as an
125 indication of the potential positive impacts of discrimination on inclusive fitness (34, 42, 43).

126

127 **Results**

128

129 **Kin discrimination**

130 We found evidence for father-son discrimination: when associating in the same party, young
131 males were in proximity and groomed with their fathers more frequently than with ‘other’ males
132 (Table 1). The ‘other’ category includes unrelated males and also paternal brothers, uncles,
133 cousins, and additional, more distant kin that, unlike maternal brothers, do not preferentially
134 socialize in male chimpanzees (44, 45; Figure 1). Consistent with previous research that
135 employed a broader age range of dyads, i.e., not limited to dyads containing at least one young
136 male (44, 45), young males were in proximity with their maternal brothers more often than with
137 other males when in association (Figure 1). In contrast to prior studies, young males did not
138 groom with their maternal brothers more frequently when associating than other males did when
139 together. Young males actually groomed with their fathers as often as with their maternal
140 brothers when associating, although they were less often in proximity (Table 1).

141

142

143 **Table 1.** Kin discrimination in social behavior. Coefficients for the effect of fathers and maternal
 144 brothers on dyadic behavior compared to ‘other’ males (including paternal half-brothers and
 145 distantly or unrelated males). Informative predictors are represented in bold typeface. Visual
 146 representation, including individual data points, is represented in Figure 1.

147

	Father ($\beta \pm SE$)	Father ($\beta \pm SE$)	Maternal Brother ($\beta \pm SE$)
Relative to Observation Time	vs. Others	vs. Maternal brother	vs. Others
Association	0.25 \pm 0.29	-0.63 \pm 0.37	0.87 \pm 0.24
Proximity	0.66 \pm 0.50	-1.40 \pm 0.651	2.06 \pm 0.42
Grooming	1.04 \pm 0.97	-0.46 \pm 1.31	1.50 \pm 0.89
Relative to Association	vs. Others	vs. Maternal brother	vs. Others
Proximity	0.76 \pm 0.30	-0.06 \pm 0.39	0.82 \pm 0.24
Grooming	2.33 \pm 0.84	2.39 \pm 1.14	-0.06 \pm 0.75

148

149 Fig 1. Social behavior patterns based on relatedness. (a) association, (b) proximity, and (c)
 150 relative to total observation time, and (e) proximity and (f) grooming relative to total association
 151 time; (d) correlation between association and proximity and grooming. Shaded boxes indicate
 152 kin categories that had positive coefficients that did not overlap with zero; statistical tests were
 153 done using multiple regression of relatedness.

154

155 **Potential inclusive fitness effects of kin discrimination**

156 Although young males were more likely to be in proximity and groom with their fathers
 157 when associating, it is unlikely that this discrimination increased the inclusive fitness of either
 158 member of the dyad (at least in the short-term – see discussion), as absolute levels of proximity

159 and grooming among father-son dyads were comparable to those between other dyads (Figure 1).
160 Nor did young males associate in parties more frequently with their fathers than with other
161 males. While it is possible that these null results represent false negatives due to lower power
162 from our small sample (N = 11 father-son pairs), this explanation is unlikely given that we also
163 found that young males preferentially associated and maintained proximity (but did not groom)
164 with their maternal brothers (N = 15 pairs) in a similarly sized sample.

165

166 **Cues underlying father-son discrimination**

167 We now turn to analyses designed to identify the cues underlying the tendency for males to
168 be in proximity and groom with their fathers when associating with them. Our first step was to
169 determine which member of the pair was responsible for father-son discrimination. Although we
170 did not collect data that would allow us to address this question for proximity, it was clear that
171 sons were responsible for the tendency of father-son dyads to groom when associating in parties.
172 Among 11 father-son dyads, 6 sons groomed their fathers, and the average number of seconds (\pm
173 SD) sons groomed their fathers per son focal hour was 12.7 ± 15.4 . In contrast, only one father
174 ever groomed his son, and the average number of seconds fathers groomed their sons per son
175 focal hour was 0.2 ± 0.7 .

176 Under the assumption that sons rather than fathers are responsible for the tendency of these
177 dyads to be in proximity and groom when associating, we next investigated how these kin biases
178 could arise if young males socialized with other males based on characteristics statistically
179 associated with paternity probability. In our first set of models ('all ages' models), which
180 employed the same age range of potential partners of young males as above, we examined how
181 the 18 young males' association-controlled proximity and grooming with 53 other males aged 8-

182 53 in 2014-2015 were independently predicted by the other males': (1) rank when the young
183 male was an infant; (2) probability of being the younger male's father based on his age at the
184 time of the young male's conception (i.e., male age-specific fertility, estimated using 15 years
185 and N = 105 paternities from long-term Ngogo data (29, 44-46)); and (3) whether the other male
186 actually was the young male's father. Our reasoning for including this third predictor variable
187 was that if father identity explains additional variation in young adult/potential father social
188 behavior even after accounting for indirect cues for paternity probability, this would suggest that
189 additional cues not included in our model may be involved in father/son discrimination. In a
190 second set of models ('potential sire age only'), we examined how the 18 young males'
191 association-controlled proximity and grooming were independently predicted by the same
192 predictors as in the models above, plus an additional predictor variable: (4) the other male's
193 association frequency with the young male's mother when the young male was an infant or
194 juvenile (~11 years previously in 2003-2004, the only period for which such archival data were
195 available). In this second set of models we only included 21 older males aged 22 - 53 years in
196 2014-2015 as potential social partners of the 18 young males. Only males of this age were ≥ 10
197 years old and reproductively active in 2003-2004 and could thus increase their chance of siring
198 the latter by associating with his mother during this time (29).

199 Young males did not maintain proximity or groom when in association with males who were
200 high ranking at the time of the young male's infancy (Figure 2). Nor did young males have high
201 levels of association-controlled proximity or grooming with older males who had frequently
202 associated with the young male's mother while he was an infant or juvenile. In contrast, there
203 was some evidence that father-son discrimination could be partly explained by the tendency for
204 young males to socialize with males who had high age-specific fertility at the time of the young

205 males' conception. This variable predicted association-controlled grooming in the 'all ages'
206 model, but not in the 'potential sire age only' model, nor did it predict association-controlled
207 proximity in either model (Figure 2). In both models, young males had higher association-
208 controlled proximity and grooming with their fathers than with other males even after controlling
209 for characteristics of males that predicted paternity.

210

211 Fig 2. Coefficients of potential cues of father-son discrimination from four multivariate models.
212 Thick lines represent ± 1 SD and thin lines for ± 2 SD. Informative predictors are represented in
213 black.

214

215 **Discussion**

216

217 We found evidence of father-son discrimination in chimpanzees, as adolescent and young
218 adult males ('young males') and their fathers were in close spatial proximity and groomed more
219 often when associating than did other dyads. While these results add to a growing body of
220 studies revealing father-offspring discrimination in promiscuously mating, group-living species,
221 they differ from most previous work in that they involved discrimination by offspring rather than
222 by fathers. This finding may seem surprising given Hamilton's (47) 'fundamental asymmetry,'
223 which suggests that because the benefits of receiving help should be higher for offspring and the
224 costs of giving help should be lower for parents, nepotism should be directed from parents to
225 offspring rather than the reverse. Hamilton's asymmetry, however, is based on the assumption
226 that actors perform behaviors for related recipients' because these behaviors increase recipients'
227 direct fitness, and thus the actor's indirect fitness. Although our results suggest that young males

228 discriminated their fathers, it is unlikely that this discrimination actually resulted in direct fitness
229 gains for fathers (and thus indirect fitness gains for young males), as the absolute amount of time
230 that young males were in proximity with and groomed their fathers was low, and not
231 significantly different from other males. Thus, father-son discrimination may occur because it
232 results in longer-term, direct fitness gains for sons.

233 How might young males increase their direct fitness by preferentially maintaining proximity
234 with and grooming their fathers when associating with them in parties? Part of the tendency for
235 males to groom their fathers when in association could be explained by young males performing
236 this behavior with males whose age difference from themselves corresponded with the
237 probability of fatherhood. At Ngogo, over 50% of offspring were sired by males age 18-26, and
238 the mean ages of fathers of young males in the current study was 40.4 years (range = 33.7 – 45.7
239 years). Socializing with these older, past-prime aged males may help young males by facilitating
240 their entry into the social network of adult males (11). During infancy and juvenility, males are
241 in near constant contact with their mothers, who serve as their primary grooming partner and
242 source of support (48-51). This changes drastically during adolescence, when males begin to
243 travel independently of their mothers and socialize with adult males. As they make this
244 transition, adolescents receive increased aggression from adult males (50) and continue to remain
245 at the periphery of parties, sometimes even after reaching adulthood (52). As a consequence,
246 adolescent males appear to be “less relaxed” and more “tense and inhibited” when they are
247 around adult males (Pusey 1990: 228). While old males are socially integrated into the network
248 of adult males, they are generally lower ranking, less aggressive, and more tolerant of young
249 males than are prime-aged males (53-57). This interpretation is consistent with research in other
250 species suggesting direct fitness benefits may sometimes play a larger role than indirect fitness

251 benefits in the evolution of kin discrimination (e.g., 58, 59, 60). For example, in many group-
252 living primates, individuals preferentially cooperate with individuals who are similar in age, as
253 cooperating with individuals who have similar needs, access to resources, and abilities to
254 exchange them results in the highest direct fitness (45, 61, 62). When patterns of male
255 reproductive skew result in age-mates being paternal siblings, individuals gain additional indirect
256 fitness benefits by socializing with age-mates as a byproduct of striving to maximize their direct
257 fitness (32).

258 Not all son-father discrimination could be explained by young males preferentially
259 socializing with old males, as association-controlled proximity and grooming was elevated in
260 young males and fathers even when controlling for the age difference between the pair. While
261 similar findings in previous studies of kin discrimination have been tentatively interpreted as
262 evidence for phenotype matching (33, 63), we must acknowledge the limitations of our cue
263 analyses. Our sample of father-son pairs was small ($N = 11$ pairs), limiting the power of our
264 multivariate analyses and the number of predictor variables we could include. For example, we
265 found that association-controlled proximity and grooming patterns of young males were not
266 predicted by the other males' association frequency with the young males' mother when the
267 young male was an infant or juvenile, but this measure of mother-potential father behavior was
268 based on only one year and one type of behavioral data. Observations across their entire period
269 of development and incorporating additional measures of social behavior between potential
270 fathers and the mothers of young males beyond association, such as proximity or grooming,
271 might yield additional insights into the cues that young males use to discriminate their fathers.

272 Irrespective of the underlying cues on which father-son discrimination is based, our finding
273 that father-son discrimination occurs in chimpanzees goes some way to bridge the gap between

274 the social and mating systems of humans and their closest living relatives. These results provide
275 support for Chapais' (13: 199) suggestion that if human fatherhood does have phylogenetic
276 building blocks in a chimpanzee-like society, "enduring father-son bonds might have been
277 initiated and maintained by the sons themselves, hence independently of and prior to the
278 evolution of active forms of paternal care." As Chapais notes, complex adaptations like human
279 fatherhood represent the end product of a multistep evolutionary sequence where progressively
280 more elaborate versions succeeded one another, and the present-day adaptive function of a trait
281 may be a poor guide for its earlier evolutionary origins.

282

283 **Methods**

284

285 **Behavioral observations**

286 A.A.S. conducted behavioral observations of adolescent and young adult males during focal
287 sampling sessions lasting one hour (mean \pm SD hours of observation per subject = 43 ± 3.2
288 hours, $N = 18$ males) from 24 August 2014 to 30 August 2015, collecting data on association,
289 proximity, and grooming. Males who encountered one another for any length of time during
290 hour-long following episodes were scored as in association with the focal subject. Individuals in
291 proximity (≤ 5 meters) to the focal subject were recorded during instantaneous point samples
292 made at 10-minute intervals. The amount of grooming given and received by focals was recorded
293 to the nearest second. Research was reviewed by the University Committee on Use and Care of
294 Animals at the University of Michigan, and was exempt because animal use was limited to non-
295 intrusive field observations.

296 To assess whether social relationships of adolescent and young adult males in 2014-2015
297 were related to social relationships they had in the past as infants and juveniles, we examined
298 adolescent and adult female and male party associations during 2003 and 2004, the one period
299 for which these data were available and collected by K.E.L (29, 64). Instantaneous point samples
300 were made at half hour intervals to record adolescent and adult males in association with focal
301 adult female subjects. Because infant and juvenile chimpanzees are in near constant contact with
302 their mothers (49) maternal party associations reflect those of their infant and juvenile sons. We
303 evaluated associations between mothers and potential fathers using the half-weight index (65) in
304 SOCPROG (66).

305 To assess the dominance status of older males, we used observations of pant grunts, a formal
306 signal of submission directed up the hierarchy and given by low-ranking chimpanzees to higher-
307 ranking individuals (67). Pant grunts exchanged between males were recorded by J.C.M.
308 between 1995 and 2004. To determine the past dominance rank of older males, we combined
309 pant grunts exchanged between males into a single giver-receiver matrix. Males were given
310 ordinal ranks (e.g. the alpha male had a rank of 1, the beta had a rank of 2). Since ordinal ranks
311 have different meaning depending on the total number of males in a given year, we controlled for
312 the number of males by subtracting the rank from the total number of males in the hierarchy, and
313 divided this by the total number of males minus one. Thus the highest-ranking male had a rank of
314 1 and the lowest-ranking male had a rank of 0 (68).

315

316 **Kinship**

317 Genetic relationships between all of our subjects are known based on prior behavioral
318 observations and genetic analyses of autosomal, X-chromosomal, and Y-chromosomal

319 microsatellite loci, and of mitochondrial DNA (29, 44, 46, 64). Eleven adolescent and young
320 adult males had fathers who were alive at the time of this study; fathers included six males.
321 Fifteen adolescent and young adult males had maternal brothers who were adolescent or adults
322 during the time of this study.

323

324 **Male age-specific fertility**

325 For every offspring born with a known father between 1 Jan 2003 and 12 Feb 2018, we
326 determined the age of the father at the time of conception, rounded to the nearest year. We
327 limited the data to infants born in or after 2003 because by this time, nearly all infants born each
328 year were genotyped. Paternities were not available for 52 of 159 infants born during this period:
329 23 infants died within 2 months of birth, and the genotypes of 9 infants born between 2017 and
330 2018 have not yet been determined. To determine age-specific fertility, we calculated the
331 percentage of offspring sired at each male age. We then calculated a 5-year running average. For
332 example, for 20-year-old males, this included the average percentage of offspring sired by 18-
333 year-old males, 19-year-old males, 20-year-old males, 21-year-old males, and 22-year-old males.
334 The running average became the male age-specific fertility value. We assigned this value to each
335 dyad based on the older male's age at the time of the younger male's conception.

336

337 **Statistical Analyses**

338 To assess social behavior between male chimpanzees, we analyzed associations, proximity,
339 and grooming interactions separately. While some researchers combine different affiliative
340 behaviors into a single index (42, 69), each behavior may reflect different aspects of social
341 behavior (70, 71) and combining them may not always be appropriate (72). Association and

342 proximity were kept as counts. Grooming was measured as a continuous variable as the duration
343 of time dyads spent receiving and giving grooming summarized across the entire year.

344 To assess the effects of kinship and examine whether a bias to socialize with fathers existed,
345 we conducted three generalized linear mixed models (GLMMs), with association, proximity, and
346 grooming between pairs of males as the outcome variables. Fixed effects were the dyads' kin
347 relationship (i.e., father-son, maternal brothers, or 'other'). The 'other' category was set as the
348 reference class. First, we constructed two models for proximity and grooming in which we
349 excluded dyads that never associated and added the log number of times each pair was in
350 association as a fixed effect to control for variation in opportunities to interact. Second, we
351 assessed absolute levels of association, proximity, and grooming for which we added the log
352 number of hour-long following episodes on the focal subject as a fixed effect to control for
353 variation in observation time. Third, to assess kin discrimination mechanisms, we constructed
354 four GLMMs, with grooming or proximity between adolescent and young adult males and other
355 males in 2014-2015 as the outcome variables. Predictors are outlined in the main text above.

356 All fixed effects were centered and z-transformed to increase interpretation of relative
357 variable importance (73). In all models, the identities of subjects and partners were included as
358 random effects. We set a negative binomial error distribution using the 'glmmADMB' package
359 (74) in R (75). We report coefficients and standard errors for each kinship category as an
360 indicator of variable importance. We considered a predictor to be informative if its coefficient
361 minus twice its standard error did not include zero.

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365 **Acknowledgements**

366

367 Fieldwork was sponsored by the Uganda Wildlife Authority, the Uganda National Council
368 for Science and Technology, and the Makerere University Biological Field Station. Nathan
369 Chesterman provided assistance in the field. For additional support, we are grateful to David
370 Watts, Sam Angedakin, Alfred Tumusiime, Ambrose Twineomujuni, Godfrey Mbabazi,
371 Laurence Ndagizi, Rachna Reddy, and the late Jerry Lwanga. For statistical advice, we thank
372 László Garamszegi and the Center for Statistical Consulting and Research at the University of
373 Michigan, especially Kerby Shedden. For helpful feedback during the development of this
374 project and comments on earlier versions of the manuscript, we thank Jacinta Beehner, Thore
375 Bergman, Anne Pusey, Brent Pav, Rachna Reddy, Sam Patterson, Bethany Hansen, Barb Smuts,
376 Kiku Adatto, Michael Sandel, Joan Silk, and additional friends, family, and colleagues of A.A.S.

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557 **Supporting information**

558

559 **S1 File. Current social behavior.** Dyadic data for adolescent and young adult males (12 – 21
560 years) with all other adolescent or adult males (≥ 8 years).

561 **S2 File. Behavioral mechanisms (‘all ages’).** Dyadic data for adolescent and young adult males
562 (12 – 21 years) with other adolescent or adult males (≥ 9 years).

563 **S3 File. Behavioral mechanisms (‘potential sires only’).** Dyadic data for adolescent and young
564 adult males (12 – 21 years) with older adult males (≥ 22 years).

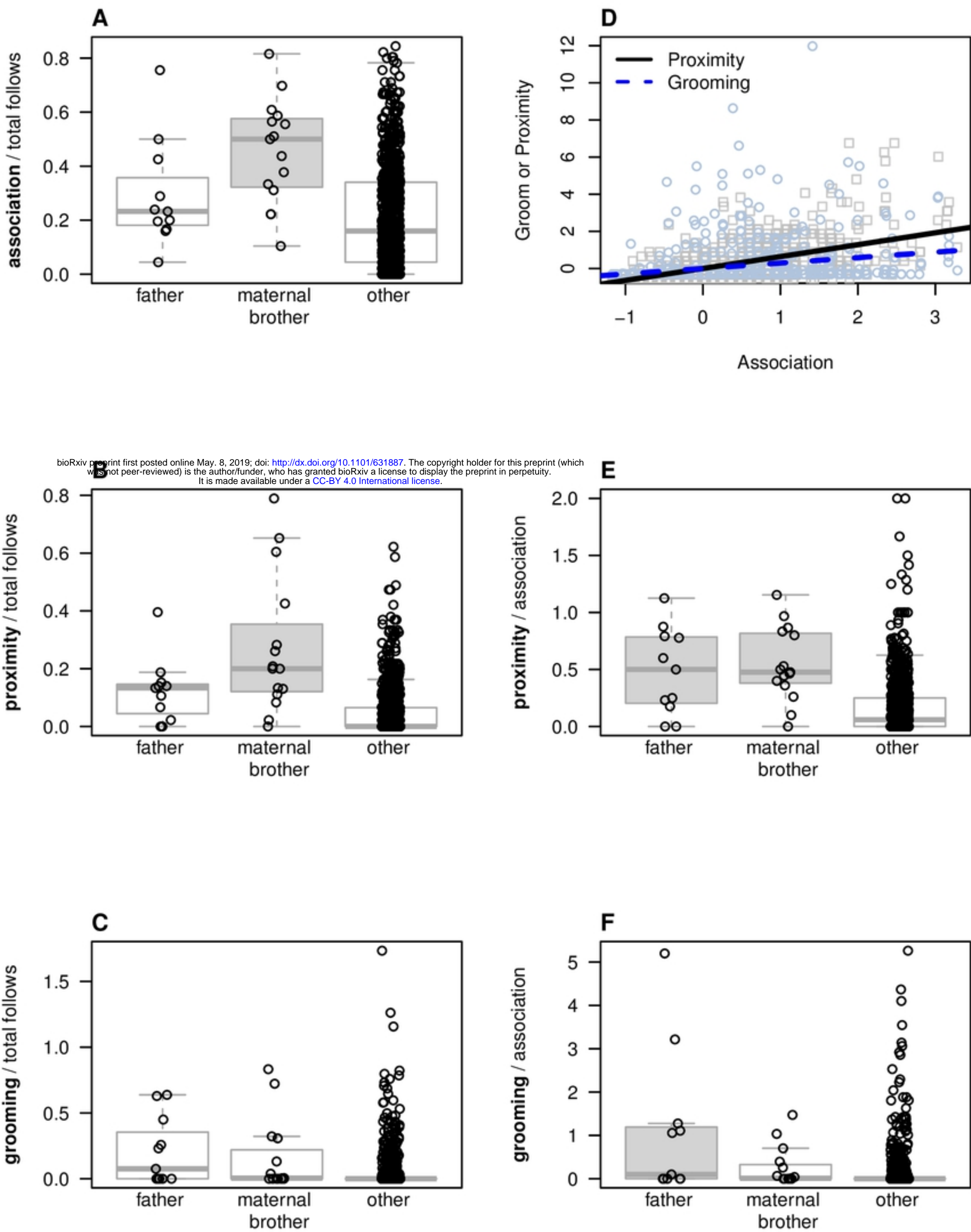


Figure 1

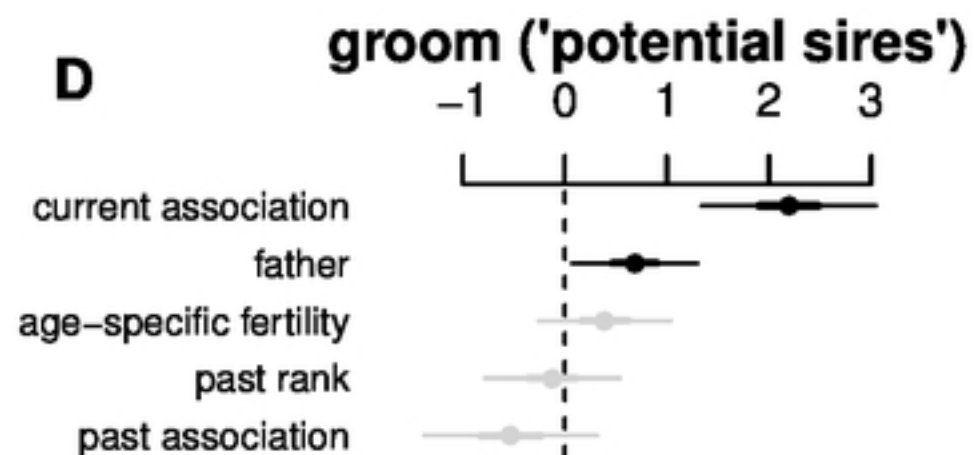
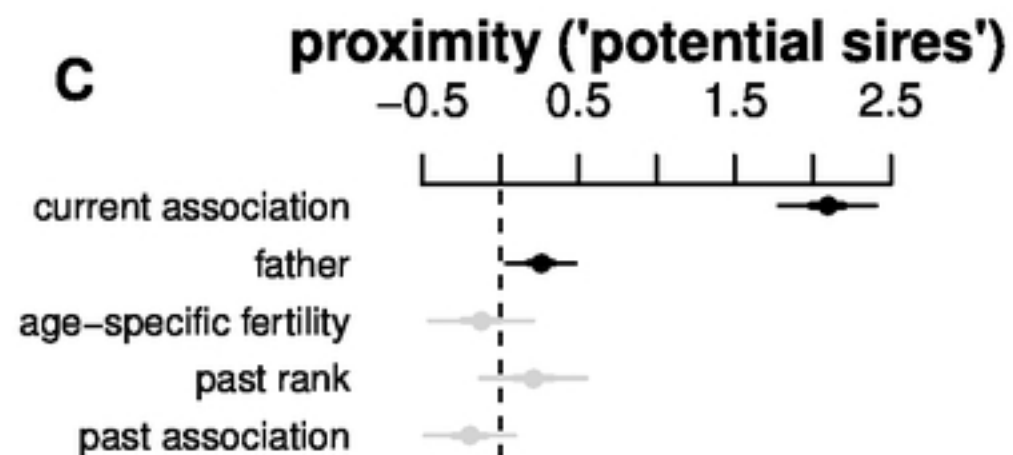
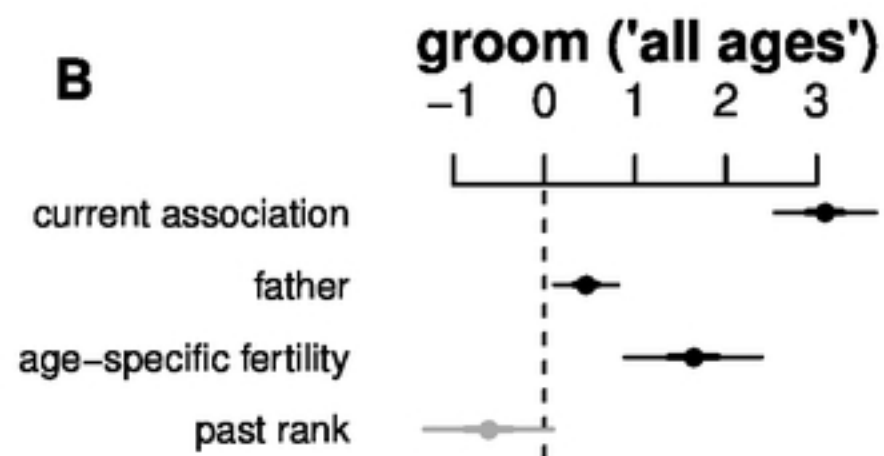
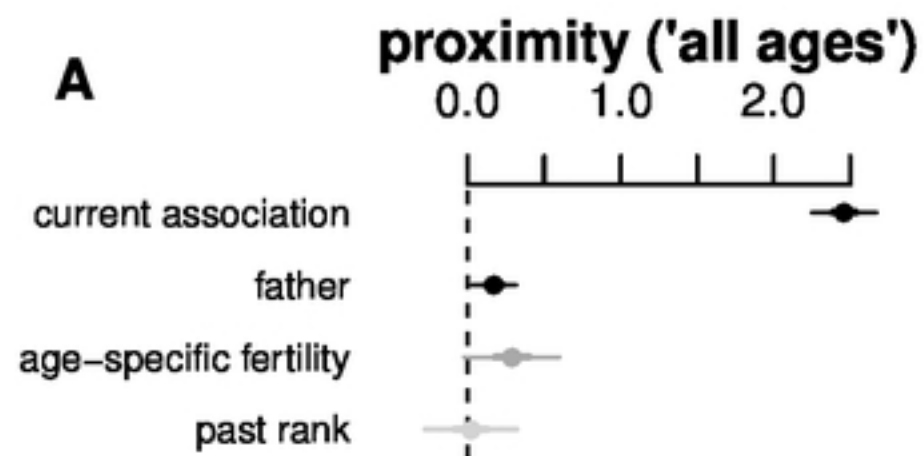


Figure 2