

1 **A network-based analysis of signal use during approach interactions across**
2 **sexes in chacma baboons (*Papio ursinus griseipes*)**

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10

11 **Abstract**

12 Greetings in primates fulfil important functions including navigation of rank, maintenance of
13 social relationships, and potentially establishing coalition partnerships. *Papio* makes a
14 particularly valuable study genus as baboons show variation in greeting, male-male cooperation,
15 philopatry, and social system. However, baboon greeting research has largely focused on male-
16 male interactions, with female approach behaviour neglected except in relation to friendships and
17 grunting. Most if not all signals seen in male-male greetings are also present in approaches
18 between other sex combinations. To understand these signals further, their use in all sex
19 combinations should be explored. We investigated approaches between male and female adult
20 chacma baboons (*Papio ursinus griseipes*), the only savannah baboon reportedly lacking male-

21 male cooperation, recorded in Gorongosa National Park, Mozambique. We compared male-male
22 greetings with those of other baboon species, identified network clusters of co-occurring signals,
23 and compared male and female approaches more broadly. Male-male approaches were similar to
24 those in other baboon species. We identified several predictable signal combinations, ear-
25 flattening with lip-smacking being a particularly strong signal of benign intent across sexes.
26 Further research comparing greeting across sex combinations and species will help disentangle
27 links between risk, cooperation, and greeting behaviour.

28 **Keywords:** greeting, proximity behaviour, grunting, lip-smacking, ear-flattening

29 **1 Introduction**

30 Baboon greeting behaviour, studied extensively for over five decades, has recently received
31 renewed interest due to the study of Guinea baboons, which exhibit highly physical and frequent
32 male-male greetings compared to other baboon species [1]. Greetings between adult male
33 baboons, which are potentially high-risk due to close physical contact, may be related to the
34 formation and testing of coalitions, and may have deeper implications for the evolution of
35 ritualized behaviour and cooperation, male tolerance, and sexual dimorphism across *Papio* [2].
36 In baboons, “greeting” refers to male-male approaches which involve some combination of a
37 swaggering gait, ear-flattening, lip-smacking, presenting, and, depending upon species, physical
38 contact behaviours including mounting, hip grasping, and genital touching [1–4]. Any further use
39 of the term “greeting” will refer only to these types of male-male encounters, in line with
40 preceding literature. We will use the terms “approaches” and “approach behaviour” more

41 broadly because we address all sex combinations and wish to avoid conflation between context
42 and potential function.

43 Approach behaviour in other sex combinations remains relatively unexplored, with the exception
44 of female grunting behaviour and its relevance for “friendships” [5–8]. Many behaviours
45 described in male greetings are also present in approaches involving females, including
46 presenting, hindquarter touches, mounting, ear-flattening, and lip-smacking, yet sex
47 combinations are usually analysed separately and rarely compared [9,10]. Studies which have
48 included females have focused on single behaviours such as hindquarter presentations [9] or
49 vocalizations [11]. Furthermore, existing greeting literature has focused on the presence or
50 absence of individual behaviours or signals, rather than the usage and meaning of signal
51 combinations. Together these issues have resulted in a poor understanding of how specific these
52 signals and their combinations are to male-male encounters and to certain *Papio* species. Failing
53 to understand these nuances makes it difficult if not impossible to address larger evolutionary
54 and communication questions.

55 “Greeting” in itself is a problematic term as it implies the function of “saying hello”, when it is
56 often difficult to differentiate between signals performed upon arrival that may have specific
57 meanings (e.g., initiate grooming) and those specific to the function of greeting [12]. Across non-
58 human primates, signals used during encounters between individuals or during merging of
59 groups have been studied in chimpanzees, mantled howler monkeys, baboons, Tonkean
60 macaques, sooty mangabeys, grey mouse lemurs, and black-and-white colobus monkeys, among
61 others [11–24]. Much of the literature focuses on interactions between approaching or passing
62 individuals, with a variety of potential underlying goals including affiliation, infant access,

63 prevention of aggression, or reconciliation [17,20,23–25]. Accordingly, the effects of rank, social
64 relationships, familial ties, and recent interaction history differ across studies. A second subset
65 focuses on interactions after separation, whether these be group-level, for example the
66 reunification of two subgroups, or individual interactions following fusion events [14,21,23].
67 The collections of signals used in an encounter can be visual, vocal, tactile, or bi/multi-modal
68 [12].

69 In baboons, higher rates of physical greeting, particularly high-risk physical greetings, are
70 correlated with increased male coalitionary behaviour and spatial tolerance, with chacma
71 baboons being the non-coalition forming outlier [2]. It has been suggested that baboon greeting
72 may be an example of ritualized behaviour and that there is a link between presence and intensity
73 of male-male greetings and social system, degree of sexual dimorphism, and male-male
74 competition [2,26–28]. In humans, rituals may enhance social cohesion, reduce competition, and
75 enforce adherence to normative values [2,29–31]. The fossil record indicates that strong
76 evolutionary parallels exist between papionines and hominins, having faced similar adaptive
77 challenges during their parallel periods of expansion and dispersal across Africa during the
78 Pliocene [32]. It is possible that similar adaptations, including those relating to cooperation and
79 social cohesion, could have allowed both clades to succeed in novel and changing environments.

80 The high level of variation in social structure, male-male relationships, cooperation, sexual
81 dimorphism, and socioecology in the *Papio* genus provides an ideal natural experiment to study
82 relationships between these factors. Six species of baboon currently range through a variety of
83 environments across Africa and the Arabian Peninsula (*P. hamadryas*, *P. papio*, *P. anubis*, *P.*
84 *cynocephalus*, *P. ursinus*, *P. kindae*), with several hybridization zones [33,34]. Their

85 environments vary drastically between and within species, which may influence signalling
86 repertoire and frequency [35,36]. While sexual dimorphism across *Papio* is relatively high in
87 comparison to other genera, chacma baboons are noticeably more dimorphic in canine height
88 than the other *Papio* species and hover at the high end of spectrum of male to female body mass
89 ratios in the genus (see table 1.1) [37–39]. Understanding how males navigate interpersonal
90 relationships, particularly in species with intense competition, is critical for studying
91 relationships between behaviour, male competition, social structure, and the evolution of sexual
92 dimorphism. Differing levels of sexual dimorphism may alter perceived risk levels in approaches
93 between different sex combinations across the *Papio* species, resulting in differences in signal
94 use. Conversely, an improved understanding of communication in close-range interactions across
95 sex combinations may provide further insight into how such interactions may shape and facilitate
96 relationships which in turn affect reproductive success.

97 The four “COKY” baboons (chacma, olive, Kinda, and yellow baboons) all exhibit multi-male,
98 multi-female groups with polygynandrous mating systems, female philopatry, and male dispersal
99 [40]. Male coalitions have been reported consistently across all COKY baboons except the
100 chacma baboon [40,41]. Limited male coalitionary behaviour was observed in one male-male
101 pair of chacma baboons by Saayman [42] and reported in chacma baboons in Gorongosa
102 National Park during hunting activity (personal communication, Susana Carvalho), suggesting
103 under-reported variation. Unlike the COKY baboons, Guinea and hamadryas baboons exhibit
104 multi-level hierarchical social structures. In both species, males are philopatric, remaining in
105 their natal clan/party, while females disperse from their natal groups [43,44]. Unlike hamadryas
106 baboons, male Guinea baboons demonstrate strong bonds with other males, with high levels of

107 male – male tolerance and affiliative behaviours such as grooming, even between less closely
 108 related males [45].

109 Table 1.1: Greeting behaviour, philopatry type, and sexual dimorphism across *Papio*

Species	Greeting exhibited	Physical contact	Philopatry Type	M-M Coalitions	Canine Height (M:F) [37, 38, 39, 43, 80]	Body Size (M:F) [37, 38, 39, 43, 80]
chacma baboon	Contested [10, 42, 50]	Unknown	Female [40, 41, 42, 83]	No [40, 41, 42, 83]	3.84	2.01
yellow baboon	Yes [9, 84]	Unknown	Female [40, 41, 83]	Yes [40, 41, 83]	2.80	1.76
kinda baboon	Unknown	Unknown	Female [81]	No [81]	3.00 [81]	1.77 [81]
olive baboon	Yes [46]	Rare [46]	Female [40, 41, 83]	Yes [40, 41, 83]	2.22	1.53; 1.85; 1.81; 1.89
hamadryas baboon	Yes [3, 47, 84]	Rare	Male [3, 47, 84]	Yes [40, 41, 83]	2.74	1.84; 1.78; 1.71
Guinea baboon	Yes [1, 27]	93.40%	Male [43]	Yes [40, 41, 83]	3.14	1.7

110 Greetings occur in hamadryas and Guinea baboons, and at a lesser rate, yellow and olive
 111 baboons [1,9,46,47]. The most ritualized and physical of greetings are exhibited by Guinea
 112 baboons; more varieties of physical contact are exhibited and physical contact is generally more
 113 frequent, intense, and risky than in the other species [1,2,27]. Greetings take on a variety of
 114 functions in male baboons, at times dependent upon the species, and may assist with in-group
 115 identification, bond testing, and relationship reinforcement (Guinea baboons) [1,27], test
 116 potential for coalitions (olive baboons) [46], or ease tension and avoid confrontation through
 117 signalling of competitive power (hamadryas baboons) [3,47,48]. Systematic study of greeting in

118 chacma baboons is limited (Tables 1.1 and 3.2), despite the importance of chacma baboons when
119 studying relationships between greeting behaviour, coalitionary behaviour, and sexual
120 dimorphism [10,41]. They are generally reported as exhibiting limited greeting behaviour, with
121 little to no physical or high-risk (i.e., genital) contact [2,10,49]. While chacma baboons do
122 exhibit some of the less intense greeting behaviours reported in other species, close proximity
123 approaches by male chacma baboons, whether towards a recipient adult male or adult female, are
124 more likely to happen without greeting behaviour than with and physical contact is rare
125 [10,42,50]. Given their status as a potential outlier among *Papio* species, further systematised
126 research on chacma greeting behaviour would be a valuable addition to the literature.

127 While most female baboon approach behaviour has been understudied, grunting is the exception
128 [6,7,51]. Suggested functions of grunting include signalling benign intent, reinforcing social
129 bonds, indicating high arousal, and reconciling following agonistic interactions [52,53]. Across
130 baboon species, grunting is more common when infants are present and may be dependent on
131 social bond strength and familial relationship [53]. Grunts may be used in a reconciliatory
132 context and interactions following grunting are less likely to be agonistic and more likely to
133 involve infant contact [5,51,52]. Differences in methodology between the female grunting and
134 male greeting literatures make direct comparison between different sex combinations difficult. A
135 more encompassing view of baboon approach behaviour would contribute significantly to our
136 understanding of the signals used during approaches, how signals are combined, and how their
137 use relates to the sex and goals of approacher and recipient.

138 **1.1 Reconsidering baboon “greeting”**

139 We find that there are three primary issues at play in the existing *Papio* approach literature. First,
140 the study of greetings does not consider females and how the same signals are used in
141 approaches between other sex combinations. Second, there is insufficient data on chacma baboon
142 approach behaviour and limited understanding of within-species variation. Third, much of the
143 existing approach behaviour and greeting literature in baboons focuses on the presence and
144 absence of individual signals, rather than considering how signals are combined. This is an issue
145 across the primate literature more broadly and makes it difficult to identify how multi-modal
146 signalling is composed and how small differences in composition modify meaning [12,54]. In
147 chimpanzees, for example, the likelihood of a reciprocal greeting is strongly influenced by the
148 modality of the initial greeting [19].

149 Here, we study approach behaviour in male and female chacma baboons (*P. ursinus griseipes*)
150 using video footage from Gorongosa National Park, Mozambique. Rather than focusing solely on
151 interactions where “greeting behaviours” were exhibited, we record proximity events (any
152 instance in which an individual comes within two meters of a conspecific after having previously
153 been more than five meters away [similar approach as in 10]). Use of this broader criterion and
154 video footage rather than *in situ* observation allows for investigation of why such behaviours are
155 exhibited in some approaches, but not others, and prevents the accidental exclusion of subtle
156 behaviours which may be missed upon first – or live – viewing. The study has three primary
157 objectives – to provide first, a further account of male-male approach behaviour in chacma
158 baboons and situate this within the existing literature; second, to look at how signals are used in
159 combination using a network approach; and third, to conduct a direct comparison of the signals

160 used in the different sex combinations, assessing how specific to male-male approaches the use
161 of the aforementioned “greeting” signals truly are.

162 We primarily applied a network analysis approach to study co-occurrence of signals across
163 varying conditions using the NetFACS package [55], originally designed for the study of
164 complex facial signals. Taking a network approach allows us to study the relationship between
165 signals themselves and between signals and specific conditions, providing a greater degree of
166 insight into the structure of approach behaviour. Each signal is treated as a network node, with
167 network edges determined by behaviour co-occurrence [55,56]. We additionally used the
168 package’s permutation test functionality to test predictions regarding differences in behaviour
169 prevalence between sex combinations.

170 Our study aims to address the following research questions and accompanying predictions.

171 1. **Research Question:** How do male-male approaches in Gorongosa chacma baboons
172 compare to the published literature?

173 **Prediction:** Based on the existing literature, we would expect chacma baboons to show
174 little to no contact behaviour, particularly intense contact, in male-male approaches when
175 compared to other baboon species.

176 2. **Research Question:** Are there specific signals which happen together more than expected
177 and do they represent different approach “types”?

178 **Prediction:** We expect to identify signal clusters that may be tied to specific sex
179 combinations or be related to specific goals (e.g., gaining infant access or receiving
180 grooming).

181 3. **Research Question:** How does the combination of approacher and recipient sex influence
182 the signals and combinations thereof exhibited during approach? Are any of the
183 behaviours which are frequently discussed in the male-male literature specific to male-
184 male approaches? These behaviours include lip-smacking, ear-flattening, presenting,
185 mounting, and hindquarter touching.

186 **Prediction:** We predict that sex combination influences the signals expected, with
187 identifiable male-male versus female-female signals, but that most signals will show
188 overlap in usage. We expect the aforementioned behaviours may be more common than
189 expected in male-male encounters.

190 **2 Methods**

191 **2.1 Study site and population**

192 Gorongosa National Park covers 3770 km² of the Urema drainage basin in the southern end of
193 the East African Rift System (EARS) [57–60]. The mosaic ecosystem results in high biodiversity
194 and makes the park a unique and valuable analogue model for the environmental conditions of
195 the EARS during important periods of human evolution [57,61,62]. The park's baboons are
196 usually categorized as chacma baboons (*Papio ursinus griseipes*), but the park lies within a
197 potential hybridization zone between northern chacma baboons and southern yellow baboons
198 [59,63]. Our study group, the Chitengo Troop, resides in the forested area surrounding the tourist
199 site and research centre and is well habituated due to continuous exposure to humans. As of
200 November 2019, the troop consisted of 8 resident adult males, 3 peripheral adult males, 1

201 subadult male, 11 adult females, 1 subadult/large juvenile female, approximately 15
202 small/medium juveniles, and an indeterminate number of infants. All adult and subadult baboons
203 were identified and named by JM in 2019 and can successfully be identified *in situ* and from
204 sufficiently high-resolution video footage. Sixty-five hours of footage were recorded
205 opportunistically during October and November 2018 and between July and November 2019 by
206 colleague Lucy Baehren and JM [64]. Recording focused on groups of baboons, with target
207 group rotated throughout the day, but was not randomized as individuals had not been identified
208 at the time of recording. Approacher identity was controlled for *post hoc*. Video recording in
209 Gorongosa National Park was completed under permit number PNG/DSCi/C145/2019 (J.
210 Muschinski) and PNG/DSCi/C110/2018 (L. Baehren) and was cleared by the University of
211 Oxford Animal Welfare and Ethical Review Board (APA/1/5/ACER/10Dec2018).

212 **2.2 Video coding procedure**

213 Footage was reviewed *post hoc* and all proximity events identified. Proximity events are here
214 defined as any instance in which one individual, the approacher, decreases the distance between
215 themselves and the recipient from over five meters to less than two meters. The proximity event
216 began once the approacher entered a five-meter radius of the recipient and concluded when either
217 1) the approacher or recipient increased the distance between each other to over five meters or 2)
218 30 second had passed since the approacher came within two meters of the recipient. In most
219 cases, the approacher could be easily identified, with one individual approaching and the other
220 remaining stationary. If both approached each other, the individual who began approaching first
221 was considered the approacher. Where an individual approached more than one stationary
222 individual, the recipient was defined as the individual who the recipient interacted with or

223 signalled towards first. If neither individual was interacted with, the first individual the
224 approacher passed was considered the recipient. Two individuals simultaneously approaching a
225 third occurred very rarely and in such situations the individual who came within two meters of
226 the recipient first was considered the approacher. Juveniles were not included in these analyses
227 because only adults and subadults could be reliably identified and identification is necessary to
228 control for potential effects of individual relationships. Events were only included if over 50% of
229 the entire sequence could be seen. The ethogram used to collect behavioural data was modelled
230 primarily after Dal Pesco & Fischer [1], Colmenares [65], and Silk [66] (for full ethogram see
231 [67]). The cleaned dataset is publicly available [68]. Behavioural data was collected using
232 BORIS version 7.10.2 [69] and data cleaning and analysis performed using Python version 3.8.5,
233 R version 4.2.2, and NetFACS version 0.5.0.

234 For analyses using NetFACS (sections 2.4 and 2.5) we included only proximity events where
235 visibility allowed for identification of the approacher's general facial expressions (e.g., lip-
236 smacking) and where both individuals were adults or subadults ($n = 341$). Future analyses will
237 focus on outcomes of these interactions and the behaviour of the recipient; this paper focuses
238 specifically on the description and identification of patterns or combinations of signals exhibited
239 by the approachers. We include only actions performed by the approacher during the approach
240 and initial interaction. The initial interaction is defined as ending once the approacher sits or
241 begins walking away, foraging, grooming, resting, or being groomed. NetFACS, used for
242 permutation tests and network analysis, requires presence/absence data for each signal of interest
243 for each event and does not account for the order, intensity, count, or length of each behaviour. It
244 compares observed probabilities to expected probabilities created using bootstrapping [55]. Prior

245 to analysis we combined several similar behaviours which had been split too finely during
246 ethogram creation (e.g., combining all non-contact threats into one category, combining all types
247 of embraces, etc.) into larger behaviour groups and we excluded any behaviours which occurred
248 in fewer than four events (1% of events) [55,70].

249 **2.3 Male-male “greeting” analysis**

250 To enable comparison with existing literature [2], all male-male proximity events were classified
251 as either “non-greetings” or “greetings” based on the presence of any traditional “greeting
252 behaviour” (lip-smacking, ear-flattening, continued direct gaze, physical contact). All proximity
253 events that could be defined as “greetings” were then assessed on three criteria - presence of any
254 physical contact (initiated by approacher or recipient), presence of intense physical contact
255 (initiated by approacher or recipient), and reciprocation. Intense physical contact has previously
256 been defined as genital touching, embracing, or mounting [1,27]. Greetings were scored as
257 “reciprocal” when the approacher and recipient both perform at least one greeting behaviour
258 [1,3]. Percentages of greetings that were physical, intense, or reciprocal were calculated in
259 relation to the count of male-male “greetings”, rather than in relation to all male-male proximity
260 events, to allow for direct comparison with the literature. It should be noted here that the total
261 number of male-male greetings reported across the 65 hours of video footage cannot be directly
262 compared to hourly rates reported elsewhere due to differences in methodology (opportunistic
263 videography vs. focal follows). We calculated bootstrapped 95% confidence intervals using the
264 boot R package [71].

265 **2.4 Identification of signal combinations - community detection**

266 To determine whether types of greeting can be identified without additional information (e.g.,
267 approacher sex), we applied community detection using the NetFACS package with a modularity
268 threshold of at least 0.3 [55,72]. NetFACS community detection uses the “fast greedy”
269 modularity optimization algorithm to determine which groups of elements co-occur more than
270 expected [55]. We completed this analysis twice – once with the dataset as prepared, with a quite
271 extensive ethogram in which behaviours are included independently (35 behaviours), and once
272 with a minimal ethogram, where behaviours are collapsed into a total of 25 categories (e.g., all
273 types of non-maternal infant contact lumped as “infant contact,” all types of non-aggressive
274 contact lumped into one category, etc.; see [67]). Each was run with 2000 randomizations, a
275 minimum significance of 0.05, minimum count of 17 (5% of 341 observations), and minimum
276 probability of 0.05. Full results of the minimized ethogram analysis are discussed below.

277 To determine whether these signal combinations were associated with specific sex combinations
278 or whether the combining of all sex combinations into one analysis hid sex-specific patterns, we
279 split the dataset into the four sex combination categories (male-male, female-female, female-
280 male, and male-female) and completed the same analysis for each subset using the minimized
281 ethogram. Minimum count cut-offs were adjusted for the subsets sample sizes. Graphical results
282 for analyses of the expanded ethogram and for the four sex combination subsets are included in
283 the supplementary information.

284 **2.5 A comparison of the specificity of “greeting” behaviours to male-male** 285 **approaches**

286 We compared the use of five signals identified in most male-male greeting ethograms (lip-
287 smacking, ear-flattening, mounting, presenting, and hindquarter touches) between male-male
288 approaches and the other sex combinations to determine whether any of these signals or their
289 combinations are specific to male-male approaches. For these analyses we compared observed
290 probabilities for each behaviour or combination of interest in male-male events to the expected
291 probability calculated from a permutation of all events (randomizations = 1000) using the full
292 ethogram with the NetFACS package. We included a random effect of approacher ID and we
293 controlled for presence of an infant not belonging to the approacher. An alpha value of 0.01 was
294 used to account for multiple comparisons. We repeated the same analysis across the remaining
295 sex combinations (female-female, male-female, female-male).

296 **3 Results**

297 A total of 428 interactions were identified from 65 hours of video footage, with 341 meeting all
298 visibility inclusion criteria (see table 3.1). The approacher was identifiable in all but 19 of the
299 qualifying interactions and the recipient in all but 18 (in 4 interactions neither approacher nor
300 recipient could be identified confidently). The mean number of unique signals included per
301 approach were 2.22 (SD = 1.47) for male-male approaches, 3.14 (SD = 2.23) for female-female
302 approaches, 2.45 (SD = 1.72) for male-female approaches, and 1.84 (SD = 1.22) for female-male
303 approaches when using the full ethogram.

304 Table 3.1: Counts of interaction types

Approacher sex		
Recipient	Female	Male
Female	167	64
Male	73	37

305 **3.1 Male-male approaches - how do the chacma baboons compare?**

306 A total of 51 male-male interactions involving only adult/subadults were identified across all 65
307 hours of footage. Of the 51 male-male proximity events, 43 can be considered “greetings”
308 according to criteria applied in other studies (presence of lip-smacking, ear-flattening, physical
309 contact, or prolonged eye contact or gaze towards) [1,2,27].

310 While Guinea baboons are certainly exceptional in terms of physical and intense physical
311 contact, it does not appear that chacma baboons are an outlier when compared to the other
312 COKY baboons (see table 3.2). Approximately 16.3% of chacma male baboon greetings
313 involved physical contact (95% confidence interval from 5.2% to 27.1%) and 9.3% intense
314 physical contact (95-CI: 0.5% to 18%), similarly to olive and hamadryas baboons. Reciprocity
315 was also similar in the chacma baboon sample and previously reported hamadryas studies
316 (estimate: 72.1%, 95-CI: 58.5% to 85.6%).

317 Table 3.2: Comparison of male greetings across baboon species

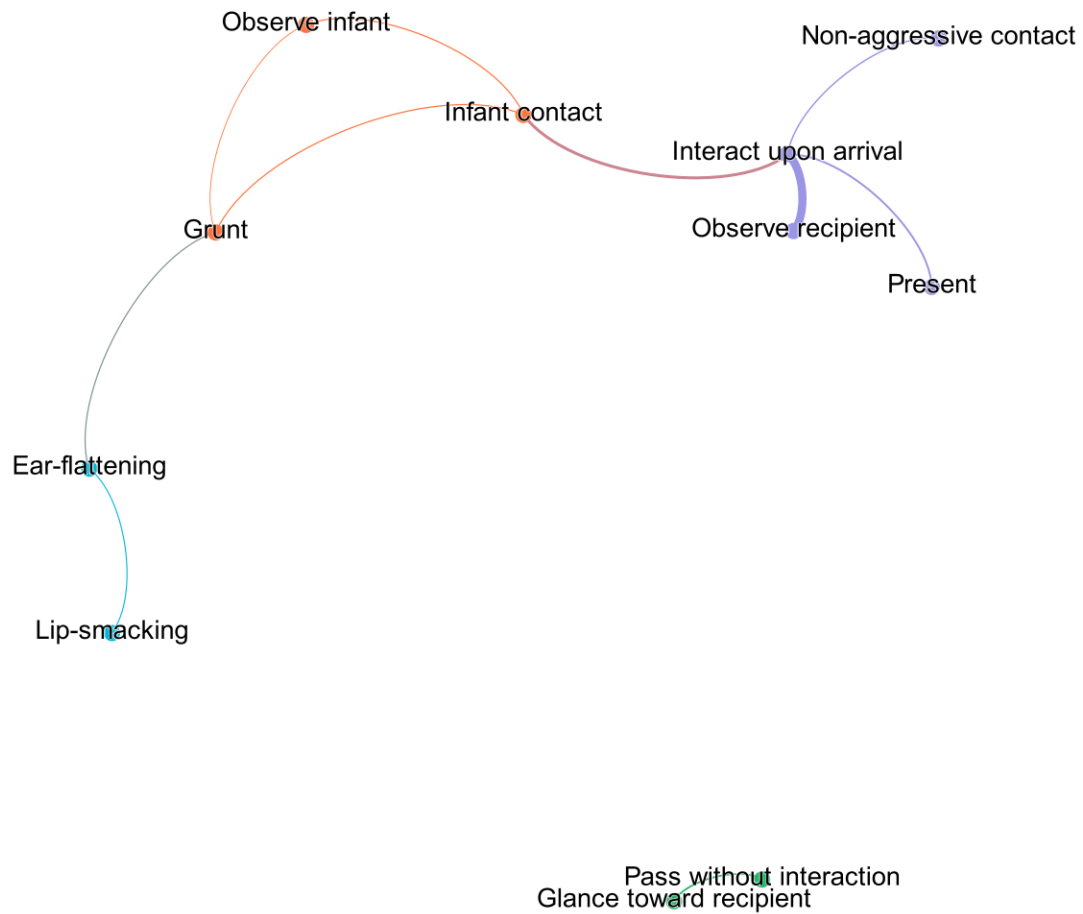
Species	Contact	Intense	Reciprocal
chacma (Gorongosa)	16.3%	9.3%	72.1%
yellow ^a	N.A.	N.A.	N.A.

Species	Contact	Intense	Reciprocal
kinda ^b	N.A.	N.A.	N.A.
olive ^c	rare	rare	N.A.
hamadryas ^d	rare	rare	71.4%
Guinea ^e	93.4%	59.2%	81.9%

^alow rate of greeting observed [9]; ^bno available data; ^c[46]; ^d[3, 47, 48, 65]; ^e[1, 2, 27]

318 **3.2 Community detection: Identification of signal combinations**

319 Community detection was completed with the larger ethogram (35 behaviours - results in
320 supplementary information) and again with a minimized ethogram (25 behaviours). With the
321 minimized ethogram, community detection identified four clusters with a modularity of 0.49
322 (Figure 3.1). The first cluster included passing without contact and glancing toward the recipient;
323 the second cluster contained observing the recipient, arriving (classified as an approach that ends
324 in the individual stopping at and/or interacting with the recipient rather than diverting or passing
325 without contact), non-aggressive physical contact, and presenting; the third consisted of
326 observing the recipient's infant, having physical contact with the infant, and grunting; the fourth
327 cluster consisted of lip-smacking and ear-flattening.



328

329 *Figure 3.1: Community detection across all greetings with a minimal ethogram. Linked and*
330 *coloured behaviours are detected clusters, with edges labelled with the combination's observed*
331 *probability. Figure created using Gephi.*

332 When the dataset was split into subsets by sex combination, clusters could be identified in each
333 subset (see table 3.3, graphical results in supplementary materials). Due to the high number of
334 female-female events, we expect community detection using only female-female events to be
335 most similar to that using all events.

336 Table 3.3: Community detection results for sex combination subsets

Sex Combination	Modularity	Clusters
Female-female	0.38	Pass without contact and glance toward
		Observing infant, infant contact, and interacting upon arrival
Male-male	0.50	Lip-smacking, ear-flattening, grunting, and non-aggressive contact
		Ear-flattening, interacting upon arrival, and observing during approach
Female-male	0.32	Grimace, present, and evasive movement
		Passing without contact and glancing toward recipient
Male-female	0.42	Observing, presenting, pausing during approach, and interacting upon arrival
		Observing, soliciting grooming, and interacting upon arrival
Male-female	0.42	Ear-flattening and grunting
		Passing without contact and glancing toward recipient

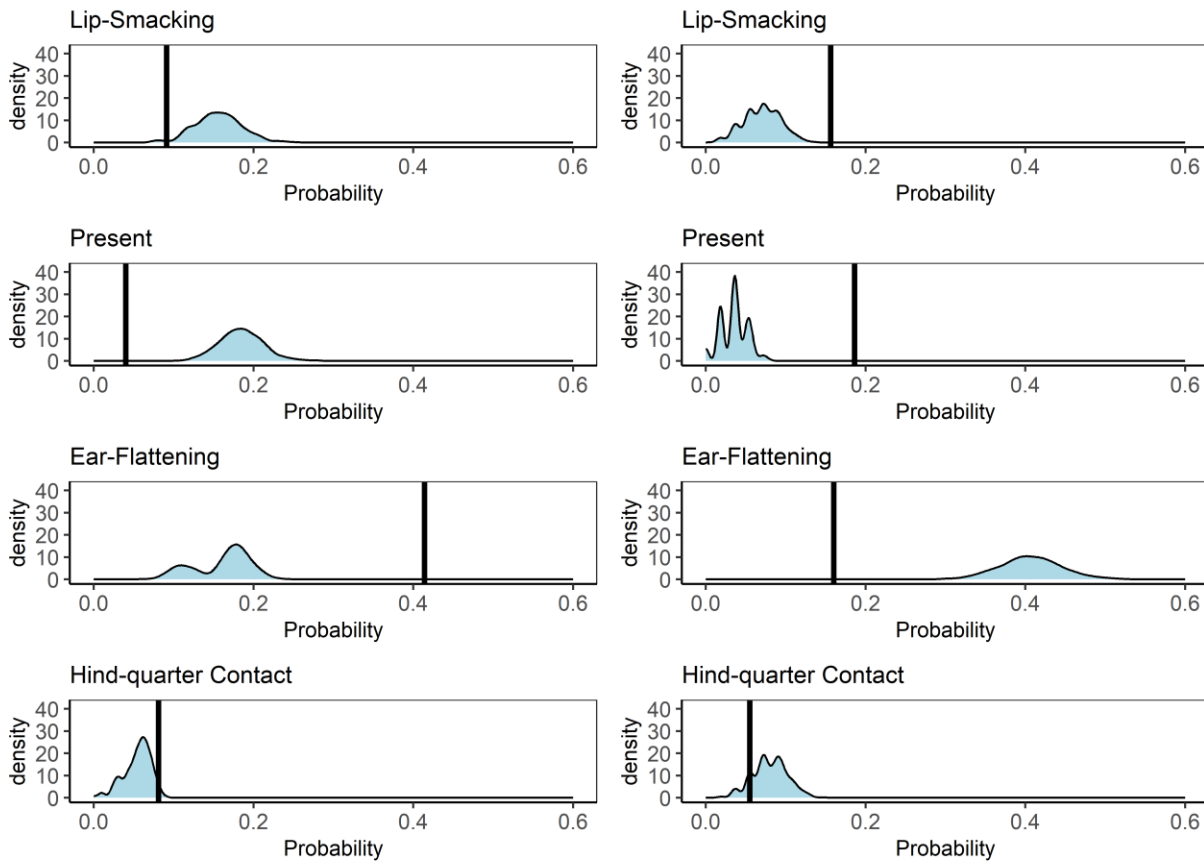
337 **3.3 A comparison of signal use in male versus female approachers and**
338 **across sex combinations**

339 The five signals we aimed to compare included lip-smacking, ear-flattening, presenting,
340 hindquarter contact, and mounting. However, due to limited occurrences and sample sizes once
341 splitting by approacher sex and by sex combination, we did not include mounting when splitting
342 by approacher sex or hindquarter contact and mounting when splitting by sex combination
343 (fewer than 4 occurrences in male or male-male encounters respectively). Given the sample sizes
344 and limited occurrences, we felt such comparisons would not be valid. However, the rarity of
345 these behaviour indicates they may not play as significant of a role as in some other *Papio*
346 species.

347 **3.3.1 Male versus female approachers**

348 When comparing observed probabilities in male approaches versus a boot-strapped sample of
349 female approaches, we found males performed ear-flattening more than expected (probability =
350 0.41, probability increase = 2.5, effect size = 0.25, specificity = 0.71, $p < 0.001$). When doing the
351 reverse, with observed probabilities in female approaches compared to boot-strapped male
352 approaches, we found females exhibited more lip-smacking and presenting than expected (lip-
353 smack: probability = 0.16, probability increase = 2.2, effect size = 0.09, specificity = 0.69;
354 present: probability = 0.19, probability increase = 5.2, effect size = 0.15, specificity = 0.88; $p <$
355 0.001 for both). Pairings of the five behaviours (for example lip-smacking with hindquarter
356 contact) were not more common than expected for either sex. While grunting was not part of the
357 original list of signals being tested, a comparison of all signals showed that the combination of
358 grunting together with lip-smacking had a particularly high probability increase of 32.2
359 (probability = 0.08, effect size = 0.08, $p < 0.001$) in female versus male approaches.

Observed vs expected probability in male (left) and female (right) approachers



360

361 *Figure 3.2: The distribution of the expected probability of four behaviours during approach*
362 *based on bootstrapped samples of the opposite sex's approach behaviours, with vertical lines*
363 *representing the observed probabilities in the sex in question (male on left, female on right)*

364 **3.3.2 Across sex combinations**

365 **Male-Male:** Separate analysis of ear-flattening and lip-smacking indicate both occur more
366 frequently than expected in approaches of male-male encounters when compared to a boot-
367 strapped sample from all sex combinations, with ear-flattening having a probability increase of a
368 factor of 2.6 and lip-smacking one of 1.8 (ear-flattening: probability = 0.53, effect size = 0.33,
369 specificity = 0.49; lip-smacking: probability = 0.22, effect size = 0.1, specificity = 4.47

370 respectively, $p < 0.001$ for both). While a comparison of all male approaches to all female
371 approaches showed no significant difference in the use of the lip-smacking and ear-flattening
372 together ($p > 0.05$), a comparison of specifically male-male approaches to all sex combinations
373 did find that the observed probability of ear-flattening and lip-smacking occurring in the same
374 approach was higher than expected in male-male encounters (probability = 0.17, probability
375 increase = 2.3, effect size = 0.1, specificity = 0.51, $p < 0.001$).

376 ***Female-Female:*** In female-female encounters, lip-smacking had a higher observed probability
377 than expected based on a boot-strapped sample of all sex combinations (probability = 0.22,
378 probability increase = 3.4, effect size = 0.15, specificity = 0.43, $p < 0.001$). In combinations of
379 size two, ear-flattening with lip-smacking had an observed probability higher than expected
380 (probability = 0.12, probability increase = 2.4, effect size = 0.07, specificity = 0.37, $p < 0.001$).
381 Though not the focus of this analysis, many combinations of infant directed behaviour, grunting,
382 lip-smacking, and ear-flattening were also present significantly more than expected
383 (supplementary information).

384 ***Female-Male:*** In female-male encounters, presenting had a higher observed probability than
385 expected (probability = 0.41, probability increase = 6.3, effect size = 0.34, specificity = 0.70, $p <$
386 0.001). No size two combinations of the five relevant signals were observed more than expected.

387 ***Male-Female:*** In male-female encounters, ear-flattening was observed more than expected
388 (probability = 0.35, probability increase = 1.68, effect size = 0.14, specificity = 0.35, $p < 0.001$).
389 No size two combinations of the five relevant signals were observed more than expected.

390 **4 Discussion**

391 Our study addresses three research themes: first, how chacma baboon behaviour fits into the
392 baboon greeting literature; second, whether signals are reliably combined; and third, in what
393 ways approach behaviour differs across sex combinations and the implications for studying
394 male-male events in isolation. The rates of intense contact, any contact, and reciprocal greeting
395 in chacma baboons are similar to those observed in olive and hamadryas baboons, indicating that
396 they may not be as extreme of an outlier as suggested by existing literature [2]. We identified
397 four clusters during community detection, suggesting that these signal combinations occur more
398 frequently than expected. Our analyses of male versus female approach behaviour highlight both
399 key differences and important areas of overlap, for example in the use of the ear-flattening and
400 lip-smacking combination.

401 **4.1 Chacmas and the *Papio* genus**

402 It has been suggested that there is little to no male-male greeting in chacma baboons and that it is
403 far less elaborate than those of other COKY baboons [10], but this impression may stem partly
404 from a lack of research on greeting in the species. Across only 65 hours of footage, we identified
405 43 “greetings,” some including hindquarter touches and even genital touching. While we cannot
406 compare rate of greeting per hour, we found that 16% of greetings involved contact, 9% intense
407 contact, and 72% are reciprocal. These align well with proportions seen in yellow, olive, and
408 hamadryas baboons (see table 3.2). Dal Pesco & Fischer suggested that male-male greeting
409 behaviour in baboons follows a geographic cline in elaboration and ritualization, with a large
410 phylogenetic split between the southern (chacma, yellow, and kinda baboon) versus northern

411 (olive, hamadryas, Guinea baboon) clades [2]. They point out that species where males are more
412 spatially tolerant and affiliative also have the highest rates of greeting and most ritualized
413 greeting behaviour, supporting suggested connections between human prosociality, larger group
414 living, and the evolution of ritual. Guinea baboons are the noticeable outlier when it comes to
415 male-male greetings, with a particularly high hourly rate, 93.4% of all greetings involving
416 contact, and 59.2% involving intense physical contact; they also demonstrate high levels of
417 male-male spatial tolerance, affiliative behaviour, and the lowest, though comparable, level of
418 sexual dimorphism in *Papio* [1].

419 Existing research on greeting in chacma baboons is limited, with early studies by Saayman and
420 Hall reporting limited presenting and contact behaviour between males [42,50]. At odds with the
421 remaining chacma literature, Saayman does report limited male-male coalitionary behaviour,
422 suggesting there may be within-species variation in male cooperative behaviour [42]. Kalbitzer
423 et al. approached the study of greeting behaviour using a similar format as here, recording all
424 approaches within one meter, and reported limited physical greeting among chacma baboons in
425 the Moremi Game Reserve, Botswana [10]. They recorded interactions as greetings only when
426 non-agonistic contact and non-affiliative contact occurred (i.e., an approach in swaggering gate
427 with lip-smacking and the come-hither face would not be considered a greeting, unlike in other
428 greeting studies), finding that greetings occurred in about 7% of close proximity approaches
429 (calculated from supplementary material [10]). The comparable rate for the Gorongosa baboons
430 is 14%. The observed percentage of Moremi Game Reserve male-male encounters involving
431 contact falls within our calculated 95% confidence interval (4% to 23%).

432 Importantly, chacma baboon male-male greeting behaviour appears to align broadly with that of
433 the other COKY baboons. This could mean that (a) their lack of coalition formation is a derived
434 characteristic and that while greetings may function to test cooperative potential in other species
435 they serve a different function in chacma baboons or are a vestigial behaviour, (b) that both
436 coalitionary and greeting behaviour is present to some degree in chacma baboons but has been
437 underestimated and understudied, (c) that greetings reflect a different aspect of relationship
438 quality which may in turn be correlated with cooperation in some but not all *Papio* species, or (c)
439 that the function of greeting behaviour has diverged across the *Papio* genus, but that a base level
440 of ritualized greeting is present across the genus and is likely ancestral. Gorongosa falls in a
441 possible hybridization zone between yellow baboons and northern chacma baboons, so we may
442 expect to see a cline in behaviour similar to the observed cline in morphology [59]. Further
443 systematic study of chacma baboon troops at different distances from the hybridization zone
444 would identify potential effects of hybridization. Gorongosa National Park provides the ideal
445 study site for such work, with 200 troops spread across 3770 km². Our study's sample size
446 prevents further in-depth comparison with other *Papio* species but does suggest that further
447 research on greeting in southern clade baboons, and particularly in chacma baboons, is
448 warranted.

449 **4.2 Signal use and combinations**

450 Through community detection, we identified four clusters of signals that occur together more
451 than expected. The first includes short glances towards the recipient and passing by the recipient
452 without contact or interaction. The second includes observing the recipient, presenting, non-
453 aggressive contact, and arriving and interacting with the recipient upon approach. The third

454 cluster includes observing the recipient's infant, having physical contact with the infant, and
455 grunting. Cluster four consists of lip-smacking and ear-flattening. Clusters two and three, and
456 three and four, are connected, with parts of this larger connected network appearing very similar
457 to clusters identified when analysing female-female events separately, suggesting that these
458 clusters may be highly related to female-female approaches involving infant contact. The cluster
459 of presenting, interacting upon arrival, and observing during the approach is likely driven by the
460 female-male interactions as it is also detected in this data subset.

461 The clustering of grunting, infant observation, and infant contact replicates findings of grunting
462 studies across several baboon species, where approachers are found to grunt more when a
463 recipient's infant is present, possibly as a way of signalling "benign intent" [6,7,51,53]. The
464 juxtaposition of the use of prolonged gaze during approaches that result in interaction (cluster 2)
465 versus the use of short glances during approaches that result in passing by without interaction
466 (cluster 1) suggest that continued observation of the recipient is a potential indicator of intention
467 to interact directly or may be a by-product of the approacher spending time assessing the
468 recipient and context. Cluster 1 (glance toward and pass without contact) appears to be largely
469 driven by female-female, female-male, and male-female interactions interactions, and cluster 2
470 (arrive and observe during approach) by male-male, male-female and female-male interactions.
471 It is possible that cluster 1 was not identified in male-male interactions due to the limited sample
472 size, and that cluster 2 was masked in female-female interactions by the high proportion of
473 infant-centered interactions. Gaze direction and length are likely associated with the outcome of
474 interactions across all sex combinations. Even if direct gaze does not serve as an intentional
475 signal, primates are generally adept at identifying when they are being looked at, suggesting that
476 direct gaze of an approacher will always serve to transmit information, even if unintentionally

477 [73–75]. The lack of further stereotypical combinations indicates there is significant flexibility in
478 how signals are combined and that approach behaviour in chacma baboons likely cannot be
479 considered “ritualized” [29].

480 **4.2.1 Ear-flattening and lip-smacking**

481 The fourth cluster - lip-smacking and ear-flattening – appears to be driven by both female-female
482 and male-male encounters, according to the observed probability of this signal combination in
483 these sex combinations compared to other sex combinations. The “come hither” or “NEEF” face,
484 which consists of ear-flattening and scalp retraction, is frequently referred to as an affiliative
485 signal in the baboon literature [8,46,76]. When comparing between male and female approachers
486 more generally, rather than splitting further by recipient sex, we find females have a higher
487 probability of performing lip-smacking and males of performing ear-flattening. This indicates
488 that signalling is very clearly affected not only by the sex of the approacher, but also by the sex
489 of the recipient. The combination of lip-smacking and ear-flattening together may be a
490 particularly strong signal of benign intent (male-male encounters can be particularly risky and
491 female-female interactions often involve attempted infant contact), used when a particular
492 outcome, for example physical contact, is desired. The clustering of the lip-smacking and ear-
493 flattening combination together with non-aggressive contact in female-female interactions
494 supports this interpretation. Ear-flattening may be more easily identifiable when observing male
495 than female approachers, but the differences in usage of lips-smacking in male-male approaches
496 and female-female approaches versus all sex combinations could not be explained by this.

497 Lip-smacking is exhibited by multiple primate species and has been found to be positively
498 associated with affiliative behaviours [54,77,78]. It is one of the most common gestures observed

499 in baboons and is used across a wide variety of contexts [79]. How lip-smacking is combined
500 with other signals influences the outcome of following interactions. In crested macaques, contact
501 after lip-smacking was found to vary based on the signals lip-smacking was combined with,
502 though ear flattening had neither a positive nor negative impact [54]. In chimpanzees, grooming
503 solicitations accompanied by lip-smacking resulted in longer grooming bouts with higher
504 probabilities of reciprocity [78]. Our results indicate that the signals lip-smacking is combined
505 with may also play an important role in baboons and lays the ideal groundwork for further work
506 investigating the outcomes and potential goals of the identified signal clusters.

507 Similar studies conducted across multiple baboon populations would help determine whether
508 sex-based differences in signal use and combination are consistent within and between species.
509 Using a network-based approach allows for a deeper understanding of the co-occurrence of
510 signals, helping us identify combinations used in specific approach contexts. This approach
511 provides further insight into how combining signals may modify meaning beyond the simple
512 sum of the signals' individual meanings.

513 **4.3 Conclusions**

514 Our results suggest that chacma baboon greeting behaviour aligns with that of the other COKY
515 baboons. Males show some contact behaviour during approaches towards other males, along
516 with many of the other reported greeting behaviours, but it is relatively rare in comparison to
517 Guinea and hamadryas baboons. Within chacma baboons, our comparison of male versus female
518 approaches suggests ear-flattening is used more frequently by males, lip-smacking and
519 presenting by females, and the combination of ear-flattening with lip-smacking is particularly
520 common in male-male and female-female encounters in comparison to other sex combinations.

521 Community detection identified several clusters of signals that co-occur and provides insight into
522 which sex combination approaches are driving the presence of each cluster. The connection
523 between lip-smacking and ear-flattening appears to be particularly relevant to encounters where
524 signalling benign intent may be especially necessary, providing a promising direction for future
525 research.

526 It is time for a widening of the study of baboon greetings, expanding past the traditional focus on
527 male-male encounters and considering approach behaviour more broadly. Including all proximity
528 events, rather than just instances where individuals “greeted” provides a more encompassing
529 view of approach behaviour and prevents omission of potentially useful information. This
530 approach will allow for more fine-tuned testing of the functions of approach behaviours;
531 knowing in which contexts interactions do not happen during an approach may be just as
532 valuable as knowing in which cases they do. This study provides an example of how widening
533 the methodological framework and using alternative analytical methods, for example network
534 analysis, can give us new insight into the specificity, context, and function of individual
535 behaviours and allow us to identify behaviour clusters used together in a robust way.

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