

35 Traditionally, animal emotional expressions have been considered
36 involuntary read-outs of signallers' internal states [1;2]. It has been assumed that
37 compared to other species, humans exhibit unmatched degrees of control over
38 their emotional expressions [3–6]. Strategic and flexible signalling of emotional
39 content has even been suggested as a key driver for the successful regulation of
40 larger social groups in early hominins and may be a potential stepping-stone to
41 conventional language [3;7–10]. However, a growing body of research challenges
42 this view, with evidence to suggest that animal emotion expressions can also be
43 produced in strategic and flexible ways and be voluntarily controlled, at least to a
44 certain extent [6;7;11]. In fact, the view that emotion expressions in nonhuman
45 animals are involuntary read-outs of internal states is invalidated *a priori* by
46 philosophical accounts that discuss emotion expressions under the logic of
47 evolutionary theories on communication [12].

48 The communication of distress may be a context where strategic emotion
49 signalling is especially important. In human toddlers for instance, producing
50 distress signals often results in emotional engagement of caregivers, including the
51 offering of consolation, a form of empathic comforting [13]. Consolation is not
52 only important for alleviating the signaller's distress, but it can also serve other
53 functions too, including strengthening of social bonds [14;15]. Given its tension-
54 reducing properties, the act of consoling an individual in distress is thought to
55 represent a behavioural marker of empathy. Consolation is quite common also in
56 other nonhuman animals, including our closest relatives, the great apes [e.g.,
57 monkeys and nonhuman great apes, henceforth 'great apes' or 'apes', 16–18;birds,
58 19;rodents, 20]. In addition to consolation, distress signals may also play a role in
59 eliciting other social interactions in post-conflict contexts, like reunions among
60 former opponents, a behaviour known as reconciliation [17], and in reducing the
61 risk of further aggression [21].

62 Thus far, consolation has been considered as a spontaneous behaviour that
63 is initiated / offered by the bystander, in the form of a physical approach [17;22–
64 24]. Although the victim's expressive behaviours prior to such an approach have
65 not yet been considered in the literature, it is likely that they may influence how
66 bystanders respond (see photo panel 1a). This would make the assumption of
67 consolation being a bystander-initiated contact more nuanced (insofar as
68 bystanders' decisions to approach to console the victim may be impacted by the

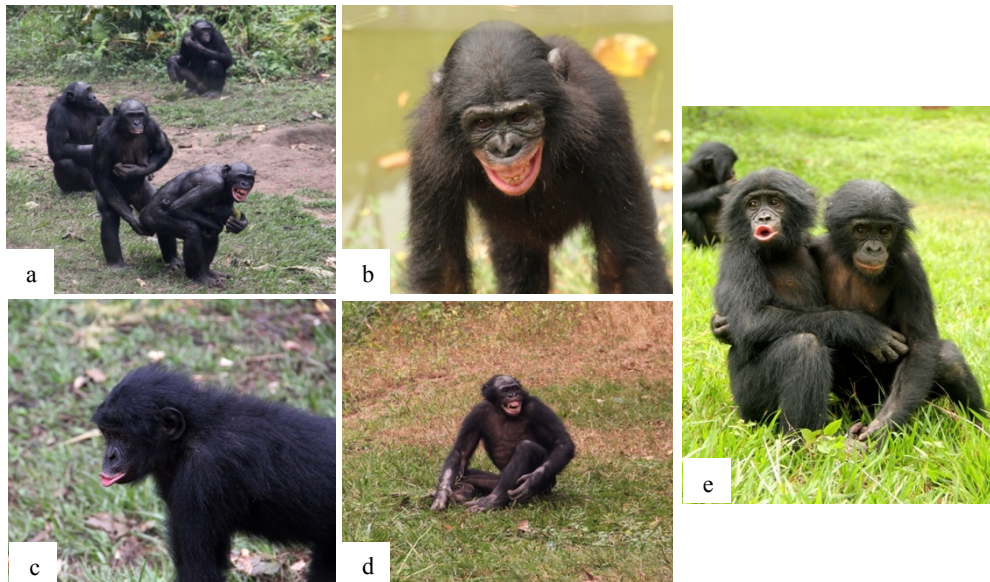
69 victims' signalling strategies preceding consolation). At present, systematic
70 evaluation of the role that victim signalling plays in shaping consolation in
71 animals, as well as for reconciliation, is missing. Overall, relatively little is
72 understood about the extent to which animals can flexibly control their emotional
73 signals for strategic goals [3;5;25] and the extent to which this capacity may be
74 human unique. Comparative data from our closest living great ape relatives are
75 crucial to gather insights into the evolution of flexible emotion signalling
76 strategies in our own species and broaden our perspective about emotional
77 intelligence of nonhuman animals.

78 One of our closest relatives, the bonobos (*Pan paniscus*), represent a
79 promising primate model to assess flexible emotional signalling strategies and its
80 link to post-conflict interactions. Apart from evidence of high levels of empathic
81 responding towards distressed conspecifics and reconciliation [17;24], bonobos
82 show apparently heightened levels of social tolerance [26], strong social
83 orientation and sensitivity towards socio-emotional cues [27–29], awareness about
84 social partners and commitments [30;31] and prosociality [32], even towards
85 outgroup individuals [33]. Bonobos are also known for their paedomorphic traits,
86 such as playfulness even in adulthood [34;35] and morphological features like
87 smaller canine teeth and juvenilized cranium [36]; these neotenous traits may
88 relate to enhanced emotionality or social sensitivity [37].

89 To advance our knowledge on the evolutionary origins of flexible
90 emotional signalling [3;7;8;38], the main goal of the current study was to assess the
91 degree of flexible and strategic emotion signalling of bonobos during a high-
92 arousal contexts, where volitional control may otherwise be presumed to be
93 relatively low [11]. To this end, we assessed how victim signalling interacts with
94 recipient behaviour, as well as with the general audience size and composition.
95 We hypothesise that if bonobos, like humans, have some voluntary control over
96 their emotion expressions, their signalling in distress contexts should be flexible
97 (socially modulated) and somewhat goal directed. Potential goals pursued by
98 victims during fights might include, for instance, receiving *consolation* from
99 bystanders (e.g., see photo 1a), repair of relationships with former opponents via
100 *reconciliation*, or *prevention of future attacks* from former opponents. To allow for a
101 multicomponent and multimodal analysis [39] of victim signalling, we took into
102 account the use of vocalisations, facial expressions, gestures (manual movements

103 produced with the limbs and head) and body signals (movements of the entire
 104 body) of victims (see photo panel 1).

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109 **Photo Panel 1.** Photographs depicting multimodal and multicomponent emotion
 110 expressions of bonobo victims following social conflicts, taken at Lola ya Bonobo
 111 Sanctuary. a) Adult female victim presenting her rump with scream face
 112 expression and victim scream vocalisation, being consoled by an adult female; b)
 113 example of bared-teeth facial expression, c) example of pout face expression, d)
 114 example of victim scream and scream face expression; d) example of victim with
 115 pout face being consoled by a juvenile bystander © Zanna Clay/ Lola ya Bonobo
 116 Sanctuary.

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118 Our first question was related to the relationship between different
 119 signalling styles and their association with post-conflict interactions. Following
 120 the literature, we distinguished between three main types of victim signalling
 121 styles: (1) *paedomorphic signals*: i.e. those resembling the signals typically used by
 122 immature bonobos to elicit care-giving responses [40–42], (2) *aggressive signals*:
 123 those with aggressive and harsh features used during tense situations or conflicts
 124 [21;43] and general (3) *affiliative-submissive signals*: those often used during
 125 submission towards, or appeasement of, dominants [6;40;44;45], see Table 1. Since

126 paedomorphic and affiliative-submissive signals are widely shown to stimulate
127 protection and assistance [e.g., in humans 46–48], we predicted that the
128 production of such signal types would enhance the occurrence of consolation and
129 reconciliation, while also reducing the risk of renewed aggression (*prediction A-*
130 *paedomorphic and affiliative-submissive signals*; see Table 2 as a summary of
131 predictions). By contrast, aggressive signals in post-conflict periods have been
132 shown to signal readiness to retaliate in chimpanzees, which has been interpreted
133 as a strategy to reduce risk of renewed aggression [21]; therefore, we predicted
134 that aggressive signals are associated with reduced risks of renewed aggression by
135 former opponents (*prediction B- aggressive signals*).

136 To explore the potential *goal-directedness* in bonobo emotion signals, our
137 next question was related to how signalling persistence is linked with potential
138 goals of victims, namely consolation and reconciliation. In doing so, we followed
139 the general assumption that signalling persistence is indicative of signallers'
140 potential goals [49–51]. Presuming that the victims' goals are to elicit consolation
141 and reconciliation, we expected that victims cease signalling after having received
142 either of such post-conflict affiliative contacts (*prediction C- goal sensitive signalling*).

143 Another research question concerned potential audience effects on bonobo
144 emotion signalling [12;52]. We predicted that, if bonobo emotion signals are
145 socially modulated, bonobos should take into account their audience while
146 signalling [12;52;53]. As there was always at least one bystander present in our
147 study, we could not test victim signalling in the absence of bystanders;
148 nonetheless we could evaluate whether signal numbers and signalling duration
149 increases with greater audience size (*prediction D – audience size*) [similar to the
150 findings of 53;54] and varying audience composition (*prediction E – audience*
151 *composition*). For the latter, we inspected the impact of close-social partners, or
152 friends. We expected victims to decrease signalling efforts with greater number of
153 friends present, as friends could increase the chance that victims receive
154 immediate support [53;55], making extensive signalling unnecessarily costly.
155 Nonetheless, we acknowledge that some studies revealed opposite effects, where
156 vocalizations increased as a function of friends' presence [56].

157 We were also interested in the developmental trajectory of victim
158 signalling. Given that limitations in cognitive maturation could affect the strategic
159 and flexible nature of animal signalling, we expected immatures to be less

160 proficient than adults in adapting their signalling based on audience size,
161 composition, and behaviour. We assumed that the flexible use of distress signals,
162 like that of any other communicative signal during play, nursing and grooming, is
163 learnt with interactional experience [57]. For immatures, we thus expected lacking
164 (or reduced) effects of signal use on consolation, reconciliation, or renewed
165 aggression (prediction A-B), of consolation on signalling persistence (prediction
166 C), and of audience size and composition on signalling efforts (prediction D-E).

167 Finally, since we are investigating flexible signalling in a highly arousing
168 distress context, we controlled for the potential impact of aggression severity and
169 piloerection [the visible erection of body hair, see 58]. There is physiological
170 evidence suggesting that piloerection indicates emotional arousal [58] and can be
171 used as indicators of arousal in primates [e.g., see 59–61]. Although there is no
172 clear direction of valence, piloerection features in a variety of high-arousal
173 contexts such as aggression [62;63], distress [61], or in humans, sadness [64] and
174 happiness [65]. If signalling is somewhat flexible, the overall signalling behaviour
175 should not be strictly tethered to two contextual and behavioural markers of
176 arousal: aggression severity or piloerection.

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178 **Methods**

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180 Study site and group

181 Observations of naturally occurring victim signalling behaviour were
182 conducted on two bonobo groups at the Lola ya Bonobo Sanctuary, Kinshasa (DR
183 Congo). Many of the bonobos living in the sanctuary were orphans rescued from
184 the bush meat trade, rehabilitated by human caregivers, and then reintegrated in
185 social groups of conspecifics. Numerous individuals were also born and mother-
186 reared at the sanctuary in their social group. For details on how we controlled for
187 victim rearing (mother-reared versus orphan) see Supplementary text 1. We
188 provide detailed information on study subjects and site in the Supplementary text
189 2 and Table S1.

190

191 Data collection

192 ZC conducted all-occurrence observations of agonistic interactions during
193 the day when the bonobos were ranging outside in their forested enclosures,

194 during two study periods [17;24]. In May-August 2011, ZC collected 301
195 observation hours with group 1 comprising 25 individuals and 152 observation
196 hours with group 2 comprising 17 individuals. From May-August 2012, ZC
197 collected 205 observation hours with group 1 comprising 22 individuals and 187
198 observation hours with group 2 comprising 20 individuals.

199 Conflicts were recorded ad libitum whenever they occurred, following
200 [17;24]. We only analysed conflicts where the victim was fully visible during the
201 entire conflict (from the start of aggression until 5 min after the conflict). We only
202 included conflicts if they involved conspecifics (conflicts involving human
203 observers were not included). We analysed $N = 144$ conflicts, which involved 27
204 victims [adult females: 5; adult males: 8; immatures < 10 years =14] and 23
205 aggressors [adult females: 9; adult males: 8; immatures (< 10 y) = 6] across the two
206 groups. We analysed communicative signals produced by victims after the
207 aggressive attacks (all age classes: $mean = 5.3$ attacks per victim, $SD = 4.2$;
208 immatures: $mean = 7.2$ attacks per victim, $SD = 4.3$; adults: $mean = 3.3$ attacks per
209 victim, $SD = 3.2$). We denoted adults as those individuals becoming (or being)
210 sexually mature and above the age of 10 years; immatures included infants,
211 juveniles, or young sub-adults below the age of 10 years (Table S1); precise birth
212 dates were not available as they were not often known for orphaned bonobos.

213 We present all further details regarding data collection methods and
214 victims / aggressors in the Supplementary text 3 and Table S1 A and B.

215

216 Video coding

217 Videos were coded in ELAN (vs. 5.7) [66]. We only coded single conflicts
218 that were independent of any other conflict event. For each conflict, we coded for
219 study year, post-conflict (PC) ID, victim identity, aggressor identity, study group,
220 aggression severity, PC events (consolation, reconciliation, renewed aggression),
221 whether victims were piloerected (i.e., fur visibly bristling from the head, neck,
222 back, or limbs, see Supplementary Image S1 and S2 for comparison), victims'
223 signalling display duration, the number of signals, their
224 vocalisation/gesture/body signal/facial expression type and style category
225 (whether they counted as paedomorphic, affiliative-submissive or aggressive
226 signal), and signalling persistence (whether victims continued signalling in
227 further bouts depending on whether having or having not received

228 consolation/reconciliation). Although self-scratching has been used previously as
229 an alternative indicator of stress in primates [67], we could not rely on this
230 measure here as conflicts were fast-paced and involved speedy movements, with
231 little occurrence of this behaviour in the immediate aftermath. For the signalling
232 persistence analysis (see section “statistical analysis”), we coded reception of
233 consolation within 1 min after the beginning of the bout (or until the next bout if
234 another bout followed within 1 min) and reconciliation within 1 min after the
235 beginning of the bout (or until the next bout if another bout followed within 1
236 min). If two post-conflict events (consolation or reconciliation) followed the bout
237 within 1 min after its start, only the first event was noted, as this was interpreted
238 to have an immediate effect on the signaller’s behaviour. Examples of how videos
239 were coded for victim post-conflict signalling can be found in supplementary
240 movies s1-s5 and supplementary audio files.

241 *Aggression severity.* We distinguished between mild and severe aggression
242 received by victims following [25]. Severe aggression occurred when aggressors
243 physically attacked victims by slapping, kicking, shoving, or biting them, or when
244 aggressors chased (pursued) victims for more than 7 m. Mild aggression occurred
245 when aggressors displaced victims without physically touching them, for example
246 by shaking, throwing, or aggressively moving vegetation, producing
247 postural/gestural threats like attempting to chase, dragging objects, or slapping
248 the ground or objects or when the chase pursuit was less than 7 m without
249 contact.

250 *Post-conflict (PC) events.* PC events could contain consolation, reconciliation
251 [17;24] or renewed aggression [21]. Following Clay & de Waal [17;24], we denoted
252 consolation when bystanders (who were not aggressors) of the PC physically
253 approached the victim to offer them friendly physical contact; this included
254 embracing, sexually engaging with, touching, playing or sitting in bodily contact
255 with the victim. We coded reconciliation when former aggressors produced
256 affiliative contact towards the victim by any behaviour(s) described above for
257 consolation, or via affiliative gestures (e.g., head nodding, hand reaching)
258 provided by the former opponent; affiliative gestures were not counted in the
259 previous literature [17;24] but were added here because aggressors’ behaviours
260 generally seemed to have a large impact on the victim’s successive behaviour.
261 Consolation and reconciliation always involved an *active* component by the

262 bystander or former opponent, respectively. Thus, for both consolation and
 263 reconciliation, we excluded cases where the victim physically approached and
 264 initiated contact, but where the recipient did not react (e.g., by clinging on to the
 265 recipient, see movie s4 at 00:25 min for a victim-initiated affiliation with a
 266 bystander that was not coded as consolation). Examples on consolation and
 267 reconciliation are provided in the supplementary movies s1-s5
 268 (<https://figshare.com/s/7dddfc02c919ec4574ef>). We coded renewed aggression
 269 as being when former aggressors re-attacked victims by displacing, taking away
 270 resources, chasing, threatening, or physically attacking the victim.

271 *Signal types.* To allow for a comprehensive and inclusive analysis of
 272 emotion signalling in bonobos, we considered all possible signal components and
 273 types [7]. We followed contemporary great ape communication literature
 274 [10;40;41;43;68–71] and produced an ethogram (see Table S2) of all gesture,
 275 vocalisation, facial expression and body signal types recorded in this study.
 276 Gestures and body signals followed at least one intentionality criteria of response
 277 waiting, audience checking and signal persistence if the goal was not met [e.g., see
 278 72]; vocalisations and facial expressions were coded by their physical form and as
 279 they occurred.

280 *Communication style.* We divided signal types (gestures, vocalisations, body
 281 signals and facial expressions) into three categories based on their form and
 282 occurrence across age as reported by the literature. We distinguished between
 283 what we denoted as: paedomorphic (P), affiliative-submissive (AS) and aggressive
 284 signals (AG), see definitions in Table 1. For a full list of each signal type's category
 285 of communication style and proportion of use across individuals, see Table S2-S3.

286

287 **Table 1.** Overview of communication styles. More information in Table S2-S3.

288

Cod	Full name	Examp	Characteristics of signal types within this
e		les	classification
P	Paedomorp hic signals	[40–42]	Signals with juvenile features, often seen in immatures of young age and in requests-to-mother, such as tantrum behaviours, pout moan vocalisation, pout face and reach gestures.

AF	Affiliative submissive signals	[21;43]	Friendly signals used in affiliative interactions, to appease others or to signal submission; often containing submissive and /or affiliative components, such as gentle gestures, self-handicapping body signals, bared-teeth expression, and victim screaming.
AG	Aggressive signals	[6;40;4 4;45]	Signals used during aggressive contexts and threats; containing aggressive or threatening components, e.g., rough gestures like slapping, punching, roughly grabbing or kicking of others, threat barks, chase-galloping.

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Signal display duration. The signal display duration was measured based on the time elapsing with the production of the first until the last signal bout following aggression. A signal bout is defined as a signalling attempt by the victim towards any bystander or the former opponents followed by a minimum of 5 sec response waiting gap (where the victim produces no further signals) [73]. The last bout was determined if there were no further signals by the victim within 2 min after. The signalling display lasted maximally 5 min, unless a signal bout was ongoing at the fifth min (in this case the recording continued until the respective bout stopped); if victims continued signalling beyond this, we did not code further, as it was unclear whether signalling would still be related to the same event with increasing time having passed.

Number of signals. We counted the number of signals following each conflict by summing all single signal components victims produced within the display duration. This meant that each signal component was counted as one signal, with signal components being either a vocalisation, gesture, body signal, or facial expression. For instance, if the victim produced multicomponent signals including a scream overlapping with a scream face, followed by a hand reach gesture that overlaps partly with an arm raise gesture, followed by a bared-teeth expression and a concave back present, we counted six individual signals. This gave us an idea about the effort in producing signals with several components while keeping

311 a degree of objectivity over what receivers would consider as one or several
312 signals (which cannot be assessed with our data).

313 *Signalling persistence after consolation/reconciliation.* We coded signalling
314 persistence after consolation and reconciliation if victims produced further signal
315 bouts, even after having received consolation or reconciliation within 1 min after
316 the bout, respectively. If instead victims had ceased signalling after these events,
317 we coded this as not persisting. As noted before, signalling bouts were defined as
318 attempts of signalling towards bystanders or former aggressors with a response
319 waiting period following that was at least 5 sec [73].

320 *Coding reliability.* The inter-rater tests on coded variables between four
321 independent coders was always more than substantial, see Supplementary text 4
322 for details and results.

323

324 Dyadic bonds

325 To assess the strength of the dyadic bonds between victims and any of the
326 potential bystanders, we calculated affiliation scores from the 10-minute affinity
327 scans which were collected on all visible individuals (see Supplementary text 3).
328 From the scans, we computed percentage affiliation scores by dividing each
329 dyads' total number of affiliation events by the dyads' total scan number,
330 multiplied by 100. To identify close social partners of the victims, we computed
331 upper quartiles from the distribution of victims' affiliation scores and checked
332 whether any of the dyadic scores fell within these upper quartiles. For any victim,
333 mothers' affiliation scores were excluded from the calculations to avoid bias of kin
334 relationships with friendship relations.

335

336 Statistical analysis

337 We used Bayesian mixed models to test our predictions [74]. We provide
338 information on how Bayesian results can be interpreted in Supplementary Text 5.

339 To test predictions, we fitted Bayesian generalized and linear mixed models
340 using the Stan computational framework (<http://mc-stan.org/>), accessed through
341 the brms package [74] (v 2.9.0) in R v. 3.6.1 [75]. Each model included four Markov
342 chain Monte Carlo (MCMC) chains, with 10,000 iterations per chain, of which we
343 specified 2,000 iterations as warm-up to ensure sampling calibration. The model
344 diagnostics revealed an accurate reflection of the original response values by the

345 posterior distributions (Fig. S2; except model 1.2 where sample size was low),
346 acceptable R-hat statistics <1.05, sufficient effective samples >100, and no
347 divergent transitions in MCMC chains (see Table S4; Fig S1). As no prior
348 knowledge was present, we used default priors (with a student's *t*-distribution of
349 3 degrees of freedom and a scale parameter of 10), see Table S4.

350 *Predictions A-B: Testing the effect of paedomorphic, affiliative-submissive and*
351 *aggressive signals on consolation (model 1.1), reconciliation (model 1.2) and renewed*
352 *aggression (model 1.3).* We could not test the prediction related to affiliative signal
353 types, as such signals were by default *always* used after attacks; there was thus no
354 variation in this predictor variable. Hence it was excluded from our models. We
355 nonetheless were able to fit three generalized mixed models to analyse whether
356 paedomorphic increased the likelihood of consolation and reconciliation, and
357 reduced risk of renewed aggression (prediction A), and whether aggressive
358 signals reduced the risk of renewed aggression (prediction B). The predictors in all
359 models were: use of paedomorphic signal types (no/yes), use of aggressive signal
360 types (no/yes), aggression severity (mild/ severe), piloerection (no/yes), victim
361 age class (adult/immature), and two interaction terms between victim age class
362 and use of paedomorphic or aggressive signal types. The dependent variables
363 were binary outcomes of consolation (see Fig. S2 model 1.1, yes / no),
364 reconciliation (see Fig. S2 model 1.2, yes/no) and renewed aggression (see Fig. S2
365 model 1.3, yes/no) within 5 min post-conflict, fitted with a Bernoulli distribution.
366 Random intercepts were modelled to account for individual variation and
367 repeated measures of victim and aggressor IDs.

368 *Prediction C: Testing the effect of consolation and reconciliation on signalling*
369 *persistence (model 1.4).* To test whether victims stopped signalling after having been
370 consoled or reconciled, we fitted model 1.4 with the dependent variable of
371 signalling persistence after receiving consolation / reconciliation (binary outcome
372 of yes/no; Bernoulli distribution Fig. S2 model 1.4). The predictors in this model
373 were aggression severity (mild/severe), piloerection during the bout (no/yes),
374 reception of consolation (no/yes), victim age class (adult/immature), and
375 interaction terms between victim age class and reception of consolation. We were
376 unable to retain the variable *reconciliation* in our model due to limited sampling of
377 data points for adults (i.e., in adults, only a total of five signal bouts were
378 immediately followed by reconciliation, and of these, only one victim persisted

379 once: LM, see Fig S3). Random intercepts were modelled to account for individual
380 variation and repeated measures of victim, aggressor IDs, and post-conflict ID (as
381 some bouts were nested within the same conflict). As opposed to the other models
382 which are based on the level of the entire victim signalling display ($N=144$
383 conflicts), this analysis is based on the level of signalling bouts ($N=329$).

384 *Predictions D-E: Testing the effects of audience size and audience composition on*
385 *signal number (model 1.5) and signal display duration (model 1.6).* To test whether
386 signal number changed with audience size [number of audience members within
387 10m (prediction D)] and composition [number of friends within 10 m (prediction
388 E)], we first fitted a generalized mixed model with the dependent variable of
389 signal number, represented as counts data (applying a negative binomial
390 distribution, see Fig. S2 model 1.5). The predictors in this model were aggression
391 severity (mild/severe), piloerection (no/yes), number of audience members
392 within 10 m (numeric), number of friends within 10m (counts), kin (i.e., mother)
393 within 10 m (no/yes), victim age class (adult/immature), and interaction terms
394 between victim age class and audience members / friends / kin within 10 m.
395 Random intercepts were modelled to account for individual variation and
396 repeated measures of victim and aggressor IDs. Similarly, to test whether signal
397 display duration (s) increases with audience members within 10 m (prediction D)
398 and friends within 10 m (prediction E), we fitted a linear mixed model with a
399 continuous dependent variable of signal display duration (applying a lognormal
400 distribution, Fig S2 model 1.6). These two models include a smaller data set
401 ($N=142$ conflicts), because data on audience composition was not present for two
402 conflicts.

403

404 **Results**

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406 Detailed information on the descriptive statistics on frequency of post-
407 conflict affiliative behaviours (consolation and reconciliation), renewed
408 aggression, signal component types (gesture, body signal, vocalization, facial
409 expression) and style categories (P, AG and AS signals) are provided in
410 Supplementary text 6.

411

412 A) Are victims more likely to receive consolation and reconciliation and less
413 likely to receive renewed aggression when producing paedomorphic and
414 affiliative-submissive signals, and does this depend on victim age?

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416 Victims were substantially more likely to receive consolation when
417 producing paedomorphic signals as compared to when not producing such
418 signals (Fig. 1A and B; $b = 1.57$, $SD = 0.77$, 95% *Credible Interval* ("CrI") [0.09, 3.12];
419 Table S4 model 1.1). By contrast, there was no clear evidence that the likelihood of
420 reconciliation increased when victims used paedomorphic signal as compared to
421 when not (Fig. 1C and D; $b = 2.55$, $SD = 1.75$, 95% *CrI* [-0.52, 6.4]; Table S4 model
422 1.2). However, this may be because of the model's low predictive power due to
423 small numbers of reconciliatory events (see Fig. S2 model 1.2). There was no
424 evidence that the likelihood of being consoled or reconciled was impacted by
425 interaction effects between age and use of paedomorphic signals (Fig. 1A and C;
426 Table S4 models 1.1 and 1.2). Yet, adults were much less likely than immatures to
427 receive renewed aggression when producing paedomorphic signals as compared
428 to when not (Fig. 1E and F; $b = 4.53$, $SD = 2.15$, 95% *CrI* [0.73, 9.22]; Table S4 model
429 1.3).

430 Our markers of arousal - aggression severity and piloerection - had no clear
431 impacts on the likelihood by which victims experienced consolation,
432 reconciliation, and renewed aggression (Table S4 models 1.1-1.3).

433 As discussed in the methods, the prediction on affiliative signal types could
434 not be tested as there was no variation in the use of affiliative-submissive signals
435 (i.e., they represented default responses to attacks).

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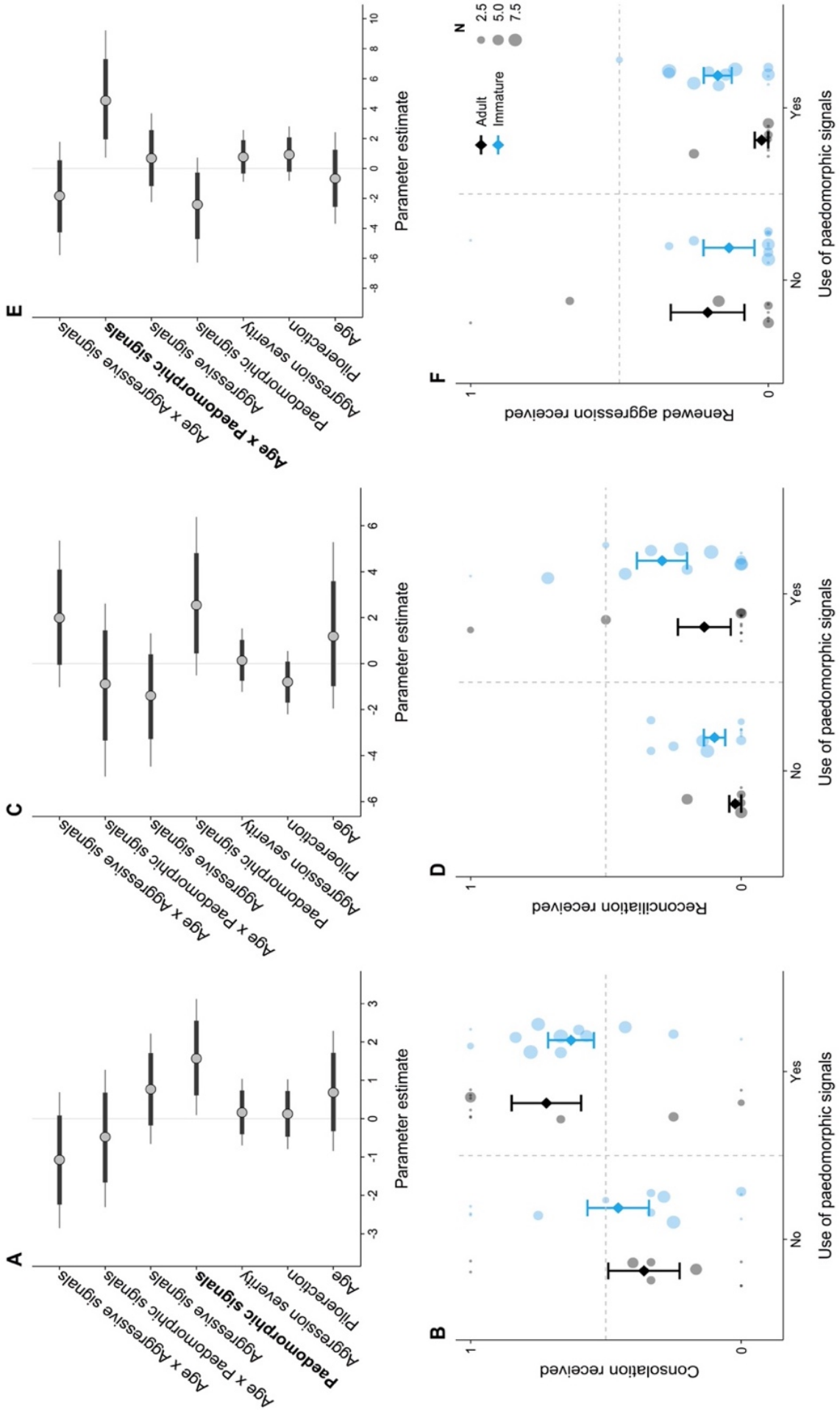
437 B) Are victims less likely to receive renewed aggression when producing
438 aggressive signals, and does this depend on victim age?

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440 The likelihood of renewed aggression was not reduced when victims used
441 aggressive signals as compared to when not (Fig. 1E; $b = 0.68$, $SD = 1.5$, 95% *CrI* [-
442 2.25, 3.68]; Table S4 model 1.3), and there were no clear differences of this effect
443 across age (Fig. 1E; $b = -1.83$, $SD = 1.91$, 95% *CrI* [-5.8, 1.78]). There were also no
444 effects of aggression severity and piloerection, see Table S4 model 1.3.

445

446



447 **Fig.1** Uncertainty intervals from MCMC draws with all chains merged for models
 448 1.1 (graph A, dependent variable: consolation), 1.2 (graph C, dependent variable:
 449 reconciliation) and 1.3 (graph E, dependent variable: renewed aggression). Points
 450 in graphs A, C and E denote posterior means, inner dark grey bands correspond
 451 to the 50% *CrIs*, and the outer fine-lined bright grey bands correspond to the 95%
 452 *CrIs*. Below are plots showing a summary of the raw data on the relationship
 453 between the proportion of having received consolation (B), reconciliation (D) or
 454 renewed aggression (F) in relation to paedomorphic signal use. Points denote
 455 proportions of victim consolation, reconciliation or renewed aggression among all
 456 observations of the victim, depending on whether these victims produced
 457 paedomorphic signals. Size of the points indicates the number of observations per
 458 victim. Diamonds depict mean proportion and upper and lower whiskers denote
 459 standard error of the mean. Bold print in graphs A, C and E indicates substantial
 460 effects.

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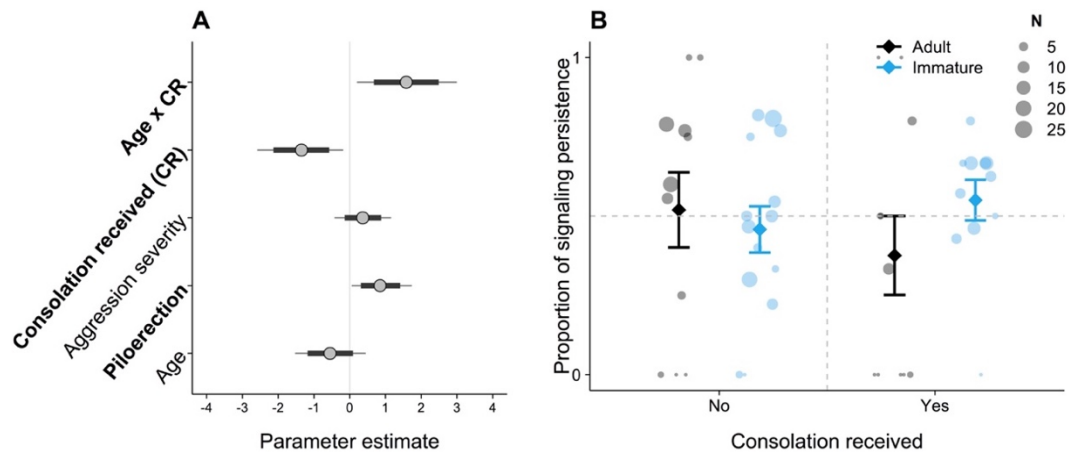
462 C) Are victims more likely to stop signalling after having received consolation or
 463 reconciliation, and does this depend on victim age?

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465 Adults, compared to immatures, were estimated to be less likely to persist
 466 in signalling after having been consoled as compared to when not having been
 467 consoled (Fig. 2A and B; $b = 1.58$, $SD = 0.71$, 95% *CrI* [0.21, 3.0], Table S4 model
 468 1.4). While aggression severity had no clear effect on signalling persistence (see
 469 Table S4 model 1.4), there was a greater likelihood of victims to persist in
 470 signalling when they were piloerected during a signalling bout compared to when
 471 they were not ($b = 0.85$, $SD = 0.43$, 95% *CrI* [0.05, 1.74], Table S4 model 1.4).

472

473



474

475 **Fig. 2** Uncertainty intervals from MCMC draws with all chains merged for model
 476 1.4 (graph A, dependent variable: signalling persistence). Points denote posterior
 477 means, inner dark grey bands correspond to the 50% *CrIs*, and the outer fine-lined
 478 bright grey bands correspond to the 95% *CrIs*. Graph B shows a summary of the
 479 raw data on the relationship between the proportion of signalling persistence in
 480 relation to consolation. The size of the points indicates the number of observed
 481 bouts per victim. Diamonds depict mean proportion and upper and lower
 482 whiskers denote standard error of the mean. Bold print in graph A indicates
 483 substantial effects.

484

485 D) Do victims produce more signals and longer signal displays when in presence
 486 of a larger audience, and does this depend on victim age?

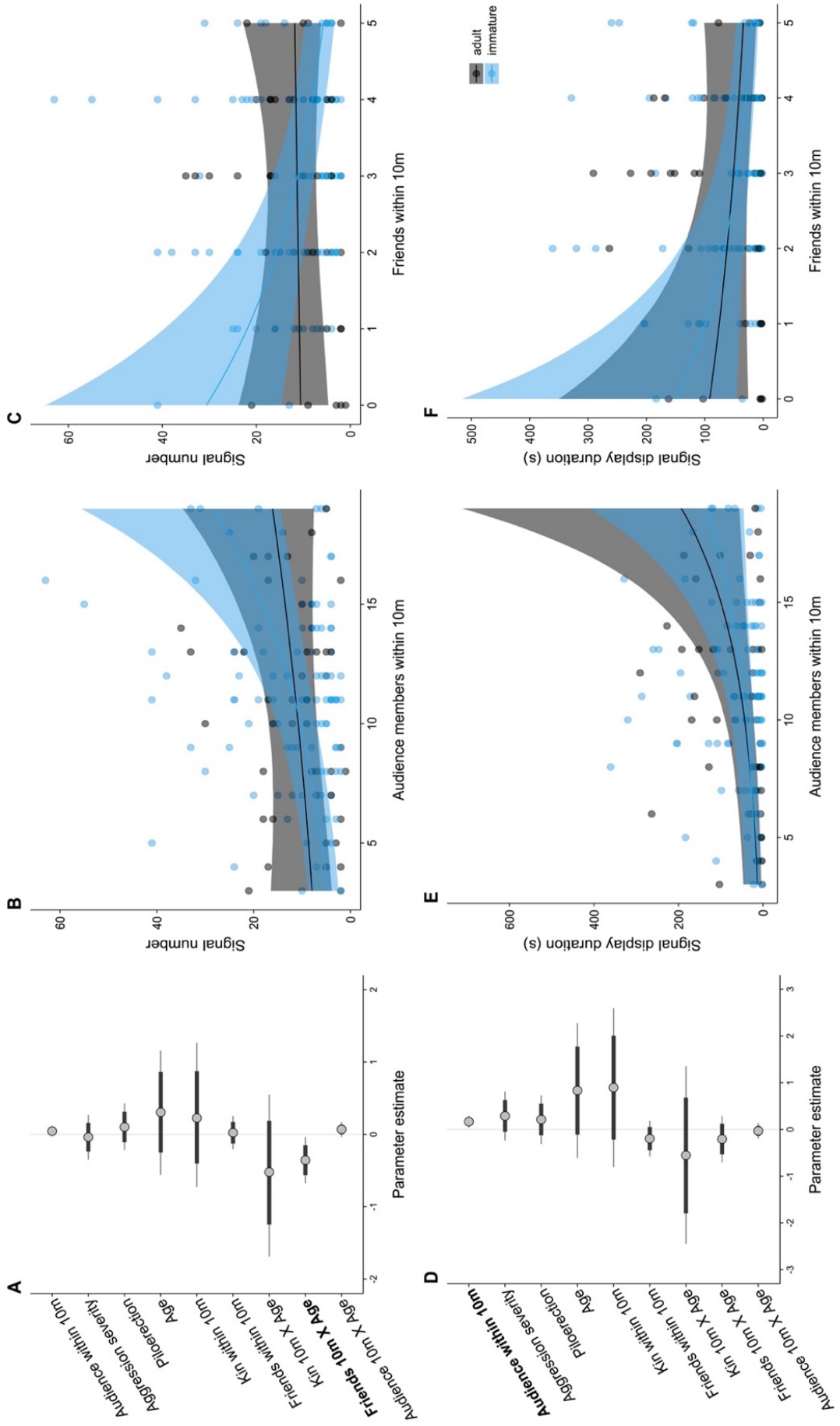
487

488 Victims tended to produce slightly more signals when audience size
 489 increased (Fig. 3A and B; $b = 0.04$, $SD = 0.04$, 95% *CrI* [-0.03, 0.12], Table S4 model
 490 1.5) with only a weak interaction term between age and audience size: immatures
 491 tended to produce slightly more signals when audience size increased compared
 492 to adults (Fig. 3A and B, $b = 0.07$, $SD = 0.05$, 95% *CrI* [-0.03, 0.17], Table S4 model
 493 1.5).

494

495 The main effect of audience became clearer when considering signal
 496 display duration: victims (regardless of age) were substantially more likely to
 497 engage in longer signal displays when audience size increased (Fig. 3D and E; $b =$

498 signalling efforts were not explained by arousal alone, as they were not affected
499 by piloerection and aggression severity (Fig. 3A and D, Table S4 models 1.5-1.6).
500



502 **Fig. 3** Uncertainty intervals from MCMC draws with all chains merged for model
 503 1.5 (graph A, dependent variable: signal number) and 1.6 (graph D, dependent
 504 variable: signal display duration). Points in graphs A and D denote posterior
 505 means, inner dark grey bands correspond to the 50% *CrIs*, and the outer fine-lined
 506 bright grey bands correspond to the 95% *CrIs*. Graphs B, C, E and F represent a
 507 summary of the raw data combined with model results on the relationships
 508 between signal number (B and C) and signal display duration (E and F) and
 509 audience members / friends within 10 m. Points denote single conflicts (i.e., one
 510 point represents signal number produced and presence of an audience in one
 511 distinct conflict). Shaded upper and lower ribbon edges depict 95% credible
 512 intervals, and the mid-ribbon-line represent estimated posterior means. Bold print
 513 in graphs A and D indicates substantial effects.

514

515 E) Do victims produce more signals and longer display durations when more
 516 friends are nearby, and does this depend on victim age?

517

518 The number of close-social partners (friends) within 10 m affected signal
 519 production more so in immatures than in adults, insofar as immatures produced
 520 less signals than adults when the number of friends within 10 m increased (Fig.
 521 3A and C; $b = -0.36$, $SD = 0.16$, 95% *CrI* [-0.68, -0.04]; Table S4 model 1.5). This
 522 effect was less clear however for signal display duration, where no clear age
 523 differences nor impact of friends could be determined (Fig. 3D and F; Table S4
 524 model 1.6). Once again, variation in signalling here could not be explained by
 525 arousal, because neither piloerection nor aggression severity clearly impacted it
 526 (Fig. 3A and D, Table S4 models 1.5-1.6).

527

528 **Discussion**

529 Our study has provided evidence that broadens the current knowledge of
 530 the strategic and flexible nature of emotional signalling in great apes, to inform on
 531 the evolutionary pathways to communicative control over emotion expressions in
 532 humans. We studied the flexibility by which bonobos communicate their emotions
 533 during distress and its relation to the behaviour of bystanders and former
 534 opponents, as well as the size and composition of the broader social audience. A
 535 key finding was that bonobo victim emotion communication is sensitive to

536 audience size and composition. Additionally, their signalling appeared to be used
 537 in potentially strategic ways to pursue specific social goals, including promoting
 538 bystander consolation and reducing the risk of renewed aggression. Signalling
 539 strategies also relied on an impressive number of multimodal signalling
 540 techniques (Supplementary text 6). Before delving into the discussion, we provide
 541 an overview of our predictions and findings in Table 2.

542

543 **Table 2.** Summary of predictions and results (see Table S4 for details on models).

544

Prediction abbreviation	Prediction*	Findings (reference to corresponding models in Table S4 and Figure)
A – Paedomorphic and affiliative-submissive signals	The production of paedomorphic and affiliative-submissive signals by victims positively predict the occurrence of consolation and reconciliation; additionally, they predict lower risks of renewed aggression. The effects should be stronger in adults compared to immatures.	Consolation by bystanders was more likely when victims produced paedomorphic signals compared to when not (no clear age differences, model 1.1, Fig. 1A and B). No clear evidence that reconciliation was affected by paedomorphic signal use (no clear age differences, model 1.2, Fig. 1C and D). Renewed aggression was less likely when victims produced paedomorphic signals as compared to when not (more so in adults compared to immatures, model 1.3, Fig. 1 E and F). We could not test any potential effect of affiliative-submissive signals due to insufficient variation.
B – Aggressive signals	Aggressive signals by victims predict reduced risk of renewed aggression.	No evidence that the likelihood of renewed aggression was reduced by the use of aggressive

	This effect should be stronger in adults compared to immatures.	signals (no age differences, model 1.3, Fig. 1E).
C – Goal sensitive signalling	Victims stop signalling after having received consolation and reconciliation. This effect should be stronger in adults compared to immatures.	Signalling persistence was less likely when consolation was received (as compared to when not), but only in adults not in immatures (model 1.4, Fig 2A and B). Reconciliation could not be tested as sample size too low (see Fig. S3).
D – Audience size	Victims increase their number of signals produced and signalling display duration with greater numbers of bystanders. This effect should be stronger in adults compared to immatures.	Only weak evidence for increased production of signal numbers with greater audience size (no clear age difference, model 1.5, Fig.3A and B), but substantial evidence for longer signal display duration with greater audience size (no clear age effect, model 1.6, Fig.3D and E).
E – Audience composition	Victims decrease their number of signals produced and signalling display duration with greater number of close-social partners present in the audience. This effect should be stronger in adults compared to immatures.	Victims produced less signals when more friends were present, yet more so in immatures than in adults (model 1.5, Fig.3A and C); no evidence for any effect of close-social partners on signal display duration (model 1.6, Fig.3A and F).

545 * *Note.* Across analyses, we controlled for presumed levels of victim arousal (via
546 aggression severity and piloerection).

547

548 Our first goal was to assess the link between different emotion signalling
549 styles and post-conflict interactions. While there were no effects of aggressive
550 signals (prediction B), we found that the likelihood of bystanders offering
551 consolation (but not reconciliation) increased when victims used “baby-like”
552 signals, in line with prediction A. Moreover, as predicted, the production of
553 paedomorphic signals in adults (as compared to immatures) reduced the risk of
554 renewed aggression by former opponents. These findings are in line with
555 empirical findings in human infants [76] and support theories on ‘cuteness’
556 selection stating that neotenous traits trigger social attention and empathy [37;47].
557 The use of paedomorphic signals in adults might be especially salient [12],
558 attracting more attention than in immatures, who already regularly emit such
559 signals. This raises the question of whether adults *retain* fixed juvenile features
560 into adulthood and are more successful due increased saliency, or whether they
561 may *intentionally* produce them as part of a flexible signalling strategy (thus, being
562 conscious about the effects such signals might have on receivers). Although our
563 observations seem to provide preliminary evidence for goal-directed emotion
564 signalling in bonobos, further experimental studies on underlying mechanisms
565 are needed to investigate these patterns. To address this, a follow-up could look at
566 whether adults actively *adjust* the signalling in relation to changes in the
567 bystanders’ behaviour. This could be done in field studies or controlled
568 experiments by testing the use of paedomorphic signals when a) receivers are
569 present but willingly (or because they are unable) refuse to provide support; b)
570 important group members suddenly arrive in the audience; c) the audience size
571 increases over time (new members arriving shortly after conflict); and d) no other
572 audience members are present who could potentially offer support.

573 More generally, the association found between distress signalling and
574 bystander consolation (widely considered a behavioural marker of empathy)
575 indicates that a bystander’s decision to console appears to be influenced by the
576 victim’s own signals prior to the approach; in other words, rather than consolation
577 being an entirely spontaneous behaviour offered by the bystander (as the
578 consolation literature suggests, e.g. [77-78]), it is more likely to involve both the
579 victim’ own expressions in response to the situation and bystander’s perception of
580 these signals and the event. Victims appear to communicate to receivers before

581 they approach for consolation. This supports the view of a more nuanced
582 interplay between the communicative signals of a distressed subject and the
583 corresponding empathic response of the receiver. In this sense, the notion that
584 consolation is a spontaneous empathic behaviour may need to be revised to take
585 into account the communicative requests provided by the victims. The possibility
586 that this form of ape prosocial behaviour is contingent on victim signalling is
587 consistent with other evidence showing that prosociality in apes may be more
588 *reactive* rather than proactive, being dependent on partner requests. For instance,
589 experimental work on helping shows that that great apes are more willing to help
590 other individuals meet their instrumental needs when explicitly requested by
591 them to do so [79].

592 To further explore the flexible nature of bonobo distress signalling, the next
593 goal was to explore the goal-directedness of victim signals. This was done by
594 looking at receiver responses and how these influenced the victims' behaviour.
595 Following previous research [50;80], we studied signalling persistence in relation
596 to consolation or reconciliation, presuming that if the bonobos cease signalling
597 following these events, this could indicate their initial goals (prediction C).
598 Indeed, we found that adults were more likely than immatures to cease signalling
599 after having been consoled, supporting the view that bonobo emotion
600 communication in adults might be somewhat strategic. Immatures' signalling
601 often continued even after consolatory events, suggesting that emotion signalling
602 in immatures might involve less control and social awareness. Although further
603 longitudinal research is needed to verify this, these findings suggest
604 developmental trajectories of emotion communication in bonobos, generating
605 exciting hypotheses related to how maternal style and early-life experiences may
606 shape emotionality in this species [17;24].

607 Although our findings provide possible evidence of strategic signalling in
608 apes, there can still be alternative explanations. For instance, persistence might
609 equally be mediated by arousal. The act of being consoled is likely to be calming,
610 which could explain why adult victims cease signalling afterwards. The lack of the
611 effect in immatures (who continue signalling even after consolation) might be
612 explained insofar as immatures may be less able to modulate their arousal
613 compared to adults. In support of an arousal-based explanation of signalling
614 persistence, we found that piloerection positively affected signalling persistence of

615 victims. This finding shows some correspondence with related work on signalling
616 persistence in wild chimpanzees and their links to arousal [54]. However, if this is
617 the case, arousal could also explain signalling persistence observed in other
618 “emotional” contexts such as social play [72;81;82], where it has been taken as
619 evidence for intentionality; although arousal is clearly a predictor of behaviour, it
620 is not mutually exclusive with intentionality, and the interplay between the two
621 deserves a case-by-case analysis [11]. Further research is needed to assess the links
622 between intentionality and arousal in conflict scenarios using careful
623 physiological data, e.g., via psycho-technological tools like infrared thermography
624 [83].

625 Lastly, to examine audience effects, we investigated signalling behaviour in
626 relation to audience size and composition (see Table 2, prediction D and E).
627 Should bonobo emotion signalling be underpinned by social awareness and even
628 voluntary control, we expected signals to be audience dependent [12]. Since at
629 least one bystander was present in all conflicts, we tested whether signal number
630 and duration increased with more audience members present (who could
631 potentially offer comfort, prediction D) and decreased when more friends are
632 close-by who would naturally offer immediate support (prediction E). We found
633 support for both predictions: victims increased their signalling efforts (by
634 producing longer signal displays) when more bystanders were present, regardless
635 of victim age. Additionally, they decreased their signalling efforts (by producing
636 less signals overall) when more friends were present, and this was more so in
637 immatures compared to adults. The unexpected age difference in relation to
638 present friends might be related to the fact that adults are less vulnerable than
639 immatures, requiring reduced sensitivity or vigilance towards surrounding
640 protectors. Although it remains unclear why immatures reacted stronger than
641 adults, our results imply an early awareness of bystander relationships in
642 bonobos. Further research is needed to investigate whether signalling to friends
643 serves a particular strategic function for younger group members.

644 Generally, emotion signals in bonobos appear to involve some flexibility in
645 usage based on social awareness. However, as before, one might argue that
646 increased signalling efforts with greater audience size (or equally, reduced
647 signalling efforts in presence of friends) could be explained more directly by
648 arousal. Yet, our data refuted this by showing that aggression severity and

649 piloerection had no clear effect on signalling behaviour. Although we looked at
650 overall audience patterns, future research might further scrutinize how victims
651 behave at the dyad-level; interesting questions to pursue would be whether
652 signalling styles differ depending on the relationship with bystanders who offer
653 consolation (social bonds and rank differences), as well as the relationship with
654 the aggressor (thus, the potential importance of reconciliation).

655 From a broader perspective, our findings also highlight unique aspects
656 about bonobo ecology and evolution. Although thought to occur in reduced forms
657 [84], bonobos, like chimpanzees, can engage in violent aggression against group
658 members [85]. Apart from socio-sexual conflict resolutions in bonobos [26;86;87],
659 flexible emotion signalling might have evolved as a tool to reduce tension and
660 avoid escalation (leading to increased social tolerance levels), especially since
661 bonobos are found to be more “nervous”, or impatient, than chimpanzees [88].
662 Although this has yet to be investigated, a way of testing this hypothesis could be
663 through an experimental comparative assessment of chimpanzees’ and bonobos’
664 ability to inhibit of negative emotions in different context (especially tense or
665 competitive ones) using thermography or hormonal analysis [89;90].

666 What do our findings mean in the context of human evolution? Turner [3]
667 suggested that across evolutionary time, the expansion and progressively
668 sophisticated social organization of early hominins might be as result of an
669 increase in complex emotions and emotion control; for instance, the control of
670 emotional outbursts could have reduced the risk of predation and increase
671 hunting success in open and dry habitats, and flexible emotion communication
672 could have facilitated more complex social interactions [3;4]. Language then in
673 turn might have further fuelled the expression of and ability to communicate
674 complex emotions, especially in the face of cooperation, favouring enhancing
675 emotional intelligence in modern humans [91–94]. In sum, our data from
676 bonobos, along with related findings from other great apes [see for a review 6],
677 suggest that the capacity to flexibly modulate signalling to pursue different
678 strategies and social goals is not a uniquely derived trait in humans, but more
679 likely was present in our last common ancestor with *Pan* [3]. It is also possible that
680 the capacity for voluntary control of emotional signals is under positive selection
681 in other species with complex social structures, also beyond the great apes
682 [6;7;95;96]; to assess the possibility of convergent evolution, comparisons with

683 other, more distantly related animal species are crucial. Moreover, although there
684 is already some evidence for flexible emotion signalling in other great apes like
685 chimpanzees [21;56], gorillas [97] and orangutans [95;98], the precise predictions
686 presented here should at least be tested similarly in chimpanzees to verify
687 whether these findings in bonobos reflect shared inheritance or evolutionary
688 convergence with humans. Being a purely observational study, our findings are
689 constrained in that we do not have direct physiological data of arousal [89].
690 Future research should use physiological data, such as infra-red thermal imaging
691 to examine how internal arousal maps onto observable signalling.

692

693 **Conclusion**

694 Results from this study provide evidence of a close interplay between
695 strategic victim behaviour and bystander prosocial responses (consolation), as
696 well as risk of renewed aggression. Our results suggest that emotion expressions
697 are not mere read-outs of internal states but can be used in flexible and strategic
698 ways to pursue social goals, even in distressing contexts. This supports the view
699 that ape emotion communication can be both arousal-driven and flexibly
700 controlled at the same time [7;11], which supports the possibility that voluntary
701 control over emotion expressions was already present in our last common
702 ancestor with *Pan*, different to what has been assumed by some [e.g., 3].

703 As well as exploring signalling strategies, our study highlights the rich
704 multimodal (e.g., sensory channels) and multicomponent (e.g., use of facial, vocal
705 or gestural signals) nature of bonobo signalling, avoiding biases as visible from
706 previous studies that focused on single components like vocalisations [99;100] and
707 facial expressions [95] in isolation. To improve our understanding of the evolution
708 of emotional intelligence, we need more comparative data assessing the flexibility
709 - as well as the various modalities and components involved - in the emotion
710 signalling of great apes.

711

712 **Data availability statement**

713 Video and audio files demonstrating communication in bonobo conflicts, as
714 well as the data and R code supporting the article can be found in an online
715 repository (figshare.com) under the link:

716 <https://doi.org/10.6084/m9.figshare.16910173.v3>

717

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728

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734

735 **Ethical statement**

736 Ethical permission was received from 'Les Amis des Bonobos du Congo'
737 (ABC) Scientific Committee and the Ministries of Research and Environment in
738 the Democratic Republic of the Congo (permit no. MIN.RS/SG/004/2009), in
739 compliance with all legal requirements for conducting research in DR Congo. This
740 study also fully complied with Emory's IACUC and Durham University's
741 guidelines for observational research with animals.

742

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