

1 **The motivation to inform others: A field experiment with wild chimpanzees**

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13 **ABSTRACT**

14 **Background**

15 Accumulating evidence indicates that some ape species produce more alarm behaviors
16 to potential dangers when in the presence of uninformed conspecifics. However, since
17 previous studies presented naturalistic stimuli, the influence of prior experience could not
18 be controlled for. ▾

19 **Method**

20 To examine this, we investigated whether apes (wild chimpanzees of the Budongo Forest,
21 Uganda) would communicate differently about a novel danger (an unusually large spider)
22 depending on whether they were with an uninformed conspecific. We tested nine adult
23 males, four of which were exposed to the danger twice alone (Non-Social group), while
24 the remaining five were exposed to the danger first alone and then in the presence of
25 conspecifics (Social group).

26 **Results**

27 We found that both alarm calling and gaze marking (i.e., persistent gaze after stimulus
28 detection) were more persistent in the Social than Non-Social group, although the effect
29 of condition only reached statistical significance for gaze marking, nonetheless suggesting
30 that chimpanzees tailored their warning behavior to the presence of others, even if they
31 were already familiar with the potential threat.

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33 Keywords: communicative motivation, wild chimpanzees, alarm calling, gaze marking

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39 INTRODUCTION

40 Converging evidence indicates that some great apes adjust their alarm behavior to the
41 putative informational needs of others (Crockford et al., 2012, 2017; Girard-Buttoz et al.,
42 2020), by communicating more frequently or elaborately when others appear to be
43 unaware of the presence of a potential threat (a model snake) nearby. Relatedly, receivers
44 expect alarm signals to be about something in their immediate surroundings, as evidenced
45 by playback studies with different species (e.g. Seyfarth et 1980, Crockford et al., 2015).
46 However, while in field experiments conducted so far (e.g., Crockford et al., 2012; Girard-
47 Buttoz et al., 2020) factors such as number of experimental exposures to a predator stimuli
48 and the presence or absence of startle responses were controlled for statistically, owing
49 to the naturalistic nature of the stimuli individuals may have differed considerably in how
50 much experience they had with the potential threat, opening the possibility that differences
51 in previous experience with the danger may account for the some of the variability in alarm
52 responses.

53
54 The ability to modify communicative signals conditional on the epistemic state of others is
55 a highly adaptive trait for social animals. This is especially the case in situations of danger
56 when knowledge states differ between members of a social group. For instance, animals
57 sometimes communicate about the presence of danger to conspecifics, even if it poses
58 no direct threat to the signalers themselves. In the wild, such a proclivity likely plays an
59 important role for safely navigating environments, including those that are subject to novel
60 anthropogenic disturbances, such as poaching or infrastructure developments (e.g,
61 Hockings et al., 2006).

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67 A number of field experimental studies have investigated this issue by placing models of
68 natural predators on the predicted travel path of wild primates to study how the discoverer
69 of the potential threat informs its naïve audience (e.g., Arnold, Pohlner & Zuberbuehler,
70 2006; Quintero et al., 2022). In one key study, Crockford et al. (2012) presented individual
71 chimpanzees with a model of a dangerous snake, which led to patterns of warning
72 behavior consistent with the callers' motivation to warn naïve group members of the
73 imminent threat. Later, a similar result was obtained by Girard-Buttoz and colleagues
74 (2020) who studied bonobos using a similar method, indicating this pattern is not limited
75 to chimpanzees. In a similar study building on the work of Crockford et al (2012) who
76 presented stimuli only when conspecifics were present, Schel and colleagues (2013)
77 presented wild chimpanzees with a dynamic (rather than static as was used by Crockford
78 and colleagues) snake model when individuals were alone or in the company of others.
79 The authors found there was no difference in alarm calling when the subject was alone
80 compared to others, suggesting alarm calling was not related to danger faced by others,
81 and found instead alarm calling was largely influenced by the presence of others with
82 whom they shared close social bonds. However, since prior experience cannot be
83 controlled in experiments presenting naturalistic stimuli, it is difficult to ascertain the extent
84 to which individuals communicate based on what others know (or do not know). For this,
85 presentation of novel threats would provide valuable insights. Such an approach would
86 enable clearer interpretations of experimental observations. For example, Schel et al
87 (2013) pointed out that uninformed individuals may have also been more likely to move in
88 the direction of the snake, meaning the calling behavior of the 'detector' may have been
89 a response to imminent danger for others based on past experiences rather than their
90 knowledge state per se. By manipulating experience, we can rule out such interpretations.

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Several scholars suggested that communication in chimpanzees and other non-human animals should be interpreted as primarily driven by affective processes (Goodall, 1986; Hammerschmidt & Fischer, 2008). Under this reading, alarm behaviors are primarily produced as by-products of the heightened arousal state of the emitter. Contradicting this proposal, however, recent evidence shows that chimpanzees cease alarm behaviors such as calling and gaze marking (i.e., persistent gaze towards the danger) when conspecifics are safely away from danger, which is at odds with this interpretation (Crockford et al., 2017; Schel et al., 2013; Townsend et al., 2017; [see Girard-Buttoz et al., 2020 for similar results in bonobos](#)). The debate is far from being currently settled, because obtaining objective measures of affective states, especially in communicative contexts, has remained an elusive pursuit (notwithstanding recent progresses in affective-state monitoring with free-ranging animals: de Vevey et al., 2022; Dezechache et al., 2017). A critical step in unveiling the proximate factors mediating alarm communication production is to experimentally isolate the alleged contribution of affect from the goal of informing others. We reasoned that, if there exists a genuine motivation in communicating valuable information to others, chimpanzees should produce communicative behaviors to uninformed others even after having been already exposed to the target referent, thus ruling out any surprise-mediated response. Differently put, provided that the stimulus is relevant to be communicated about to a potential audience, we should expect communication to occur in animals already aware of the target, and thus not immediately aroused by it, if their communicative behavior indeed reflects a motivation to inform others. In such a case, communicative behavior should be primarily affected not by the signaller's

Deleted: A design feature of the Crockford et al 2012 and similar studies (e.g., Crockford et al., 2017; Girard-Buttoz et al., 2020) is that the predator models are presented on just one single occasion. Although this prevents animals from habituating to the danger stimulus and realizing its non-threatening nature, it also presents a drawback: namely, it leaves open the question to what extent the observed warning behaviour

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familiarity to the target stimulus, but by the knowledge state of the putative audience.

While previous studies (e.g., Crockford et al., 2012; Girard-Buttoz et al., 2020) controlled for surprise by including startle responses as a control variable in statistical models or in some cases conducting multiple trials in the same location, no studies have experimentally controlled for surprise, which would require multiple within-individual presentations of a novel stimuli.

To explore this, we designed a study in which N=9 wild male chimpanzees of the Budongo Forest Reserve in Western Uganda were first exposed alone to a novel animal model (a spider, which is naturalistic, but entirely novel since no such animal is found in the territory of our study community). All of them were then presented a second time with the spider.

However, during their second exposure N=5 subjects were in the company of naïve community members (Social Group), whereas the remaining N=4 subjects were tested alone for a second time (Non-Social Group). If chimpanzee alarm behavior is mainly a direct response to external threats, then the second exposures should uniformly lead to weaker responses, regardless of the presence or absence of a naïve audience. Instead, if chimpanzees are motivated to inform others, regardless of their own inner state, we expected subjects in the Social Group to show significantly more alarm behaviors compared to those in the Non-Social Group, despite equal familiarity with the spider.

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158 **METHODS**

159 **Ethical note**

160 Permission to conduct the study was granted by the Ugandan Wildlife Authority (Permit
161 ID: COD/96/02) and the Uganda National Council for Science and Technology (Permit ID:
162 NS599). The Sonso community has co-existed with humans for many decades. Its home
163 range covers a large estate of an abandoned sawmill, the Budongo Conservation Field
164 Station, and various settlements along the forest border. Individuals therefore regularly
165 encounter human artifacts, some of which pose a grave threat, such as wire snares,
166 mantraps and weapons used by farmers to drive away wildlife. All work complied with
167 international standards such as the Association for the Study of Animal [Behavior](#) (ASAB)
168 ethical guidelines and the UK Animal Scientific Procedures Act 1986, including taking all
169 possible measures to follow the 3R tenets by using a design that required the fewest trials
170 possible to answer the research question and limiting our study to a sub-sample of the
171 overall population (i.e., focusing only on male chimpanzees). We also followed taxon-
172 specific guidelines, namely, the International Union for the Conservation of Nature's Best
173 Practices for working with Great Apes.

174

175 **Study site**

176 The study was carried out in the Budongo Forest Reserve, a moist semi-deciduous
177 tropical forest in western Uganda, covering 428 km² at an altitude of 1,100 m, between
178 1°35' and 1°55'N and 31°08' and 31°42'E (Eggeling, 1947). Data were collected in the
179 Sonso community between May 2015 and June 2015, and between April 2016 and May
180 2016. Habituation of this community to humans began in 1990, with the majority of
181 individuals (approximate N = 70) well habituated to human observers (Reynolds, 2005).

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184 **Individuals**

185 Although more gregarious than females, males were more likely to be found travelling on
186 their own, while females are typically accompanied with offspring (and other females when
187 nulliparous). For this reason, we focused on males, and considered all the adult males of
188 the community at that time (N=13). Two of them disappeared between the start and the
189 end of the study. Two additional individuals could not be tested. One was never leaving
190 the main group on its own as he was the alpha male over the course of the study. The
191 other was not well habituated and showed signs of nervousness when being followed. We
192 were thus left with N=9 individuals.

193

194 **Procedure**

195 Figure 1A-B sums up the procedure. Individuals were distributed into two groups: the
196 Social (N=5) and Non-Social (N=4) groups. Field conditions prevented random subject
197 allocation to the two groups. The individuals that were more likely to be found alone were
198 selected to be part of the Non-Social group. This introduces a potential confound which
199 we will elaborate on in the Discussion section.

200

201 All individuals were tested twice. In the first trial, individuals were alone (i.e., no other
202 individual was present within a 30-meter radius for at least 30 minutes and no calls from
203 community members had been heard from within 100 meters for at least 10 minutes). In
204 the second trial, individuals from the Social group were tested with at least one member
205 of their community present within a 30-meter radius. Individuals from the Non-Social group

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213 were re-tested alone. The gap between the two trials was 10.57 days (+/- 15.30 SD) on
214 average.

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216 Each trial consisted in the presentation of a mechanical spider to the focal individual (as
217 done in Dezecache et al., 2019). The spider was set at around 7-meter distance from the
218 animal and operated for duration 18.45 seconds (+/- 8.35 SD). This model represents a
219 species absent to the fauna of the Budongo Forest reserve, meaning it represents a
220 stimulus worth communicating about even if not immediately dangerous. To avoid
221 chimpanzees inferring that the decoy spider was a human artifact, we carefully avoided
222 manually interacting with it when in the presence of our subjects. We ensured the target
223 saw the spider first by placing it closest to them.

224
225 In a pilot experiment (conducted a month prior), we exposed 4 male chimpanzees (N=2
226 from each group) to the spider and found that it elicited hoo alarm calls in all subjects,
227 thereby suggesting that it was perceived as a likely threat. Because of this pilot, it may be
228 argued that those 4 chimpanzees had an increased exposure to the target stimulus. This
229 is unlikely to represent a confounding issue, for two reasons: firstly, there was a month-
230 long time interval between pilot and experiment; secondly, all individuals started with an
231 'alone' trial when the experiment began, and the statistical comparison is being made
232 between the 2 experimental trials for each individual of both groups.

233
234 **Coding**

235 As main alarm responses, we considered startle/alert hoos (Crockford et al., 2012, 2018;
236 Schel et al., 2013) and alarm barks (Crockford & Boesch, 2003). We also examined the

gazing behavior, since vigilance or gaze-alternation patterns are known to be modulated by communicative goals (Crockford et al., 2017; Dezechache et al., 2019; Schel et al., 2013). Specifically, since chimpanzees are adept gaze-followers (Call et al., 1998), we reasoned that participants could manipulate others' attentional states by maintaining gaze towards a relevant stimulus. This is consistent with marking behavior seen in chimpanzees upon encountering a snake (Crockford et al., 2017).

We coded whether there was calling behavior (yes = 1; no = 0) by the subject from detection up to 30s. We also coded from the videos using software BORIS (v8.5, Friard & Gamba, 2016) the amount of time the subject was looking (i.e., gaze marking) at the spider from detection up to 30s. In the two trials of the individual PS looking time measurement was interrupted after ~16.5 and ~25 seconds respectively because the individual moved location and was not in a position to see the spider anymore. Visual examination from the refuge location was done immediately after the trial to confirm this. To avoid disparities across individuals, we divided the looking time by the total possible looking time (usually 30 seconds, except for the two trials involving PS), and obtained the proportion of looking time within the possible looking time window for each individual and each trial.

Inter-rater reliability test based on N=17 trials found consistency between GD and two naive observers on looking duration (Single Score Intraclass Correlation: ICC(C,1) = 0.828; $F(16,32) = 15.5$; $p < .001$). One trial was discarded for this test because the two naive observers did not pay attention to the event of interest (i.e., the spider beginning movement). Raters were also consistent on how long the spider was activated for

260 (ICC(C,1) = 0.996; $F(16,32) = 781$; $p < .001$). Note that, since alarm calls can be very soft
261 in chimpanzees, they were coded live together by GD and SA and/or MM.

262

263 ***Statistical analysis***

264 Statistical analyses were conducted using R (v. 3.5.1, R Core Team, 2020) and RStudio
265 (v. 1.1.456, RStudio Team, 2020). To test for a Group effect on call production and gaze
266 marking in trial 2, given the call baseline obtained in trial 1, we ran general linear mixed
267 models with a binomial distribution using function 'glmer' of package 'lme4' (v1.1.23; Bates
268 et al., 2007). The dependent variable for calling was whether calling occurred or not and
269 for gazing was whether the subject gazed or not in the 30 seconds following stimulus
270 detection. The models included predictors 'Group', whether calling occurred or not at trial
271 1 (for the vocal warning model), proportion of time spent looking at the spider in trial 1 (for
272 the gaze marking model), the delay between trials 1 and 2 (in days) ('Delay'), and the
273 length of spider activation in the two trials (in seconds) ('Spider movement duration at trial
274 1' and 'Spider movement duration at trial 2'). Although similar studies controlled for startle
275 responses (e.g., Crockford et al., 2012) we decided not to control for this variable in our
276 model owing to a small number of cases of startle responses (see supplementary table
277 S1). To investigate the effect of Group, we compared our full model with a null (intercept-
278 only). Our statistical procedure was the same for testing a Group effect on gazing at the
279 spider.

280 Before models were run, we transformed (log-transformation followed by z-scoring)
281 predictor 'Delay' because its distribution suffered from right-skewedness. We also z-
282 scored predictors 'Spider movement duration at trial 1' and 'Spider movement duration at
283 trial 2'.

RESULTS

Vocal warning

During the first exposure to the spider model, 5 of 9 alone subjects produced alarm calls (3 of 4 non-social group and 2 of 5 social group subjects). During the second exposure, the proportion of calling individuals in the Non-Social Group decreased from 3/4 to 1/4 subjects, whereas in the Social Group, calling increased from 2/5 to 3/5 subjects (Figure 2A). All calls were alarm hoos (Crockford et al., 2012, 2015, 2018), in addition to one pant-hoot call (Fedurek et al., 2016) produced by individual KT (Social group) on trial 2. Although the patterns observed are anecdotally consistent with our predictions (see Figure 2A), our full model was not statistically better than the null model (Type II Wald chisquare tests: $X(4) = -2.65$; $p = .61$). The full model summary is shown below in table 1 and raw data are shown in table S2

Gaze marking

During the first exposure, the mean looking duration at the spider was 21.07s \pm 7.86s (Mean \pm SD), with no obvious differences between the subjects assigned to Social and Non-Social groups (Social = 22.2s \pm 7.81s vs. Non-Social = 21.4 \pm 9.17; Means \pm SDs). During the second exposure, looking duration decreased overall to 15.98s \pm 6.71s (Means \pm SDs), especially in the Non-Social group (Social = 18.8s \pm 3.38s vs Non-Social = 9.75s \pm 2.43s; Means \pm SDs). Correspondingly, our full model was significantly better than the null model (Type II Wald chisquare tests: $X(4) = 29.37$; $p = <.001$). The full model summary is shown below in table 2 and raw data are shown in table S3.

309 Post-hoc tests showed that, at first exposure, looking time did not differ between groups
310 (t ratio test: t-ratio = 0.16; p = 0.87) but a significant difference emerged at the second
311 exposure, with looking time being higher for the Social than Non-Social group (t ratio =
312 2.22; p = 0.046, d = 2.80), a result which is significant with a two-tailed test without
313 correction for multiple comparisons (in that case, two comparison). All other model factors
314 (Group, Delay between trial 1 and 2, duration of spider activation) were non-significant (all
315 ps > .1). Looking time data are shown in Figure 2B.

316

317 **DISCUSSION**

318 We asked whether the presence of an uninformed audience increases the motivation in
319 wild chimpanzees to communicate about an unfamiliar and potentially dangerous target,
320 which the signaler had already been exposed to. We adopted an experimental approach
321 wherein we presented nine subjects with a potential threat twice, first in private without
322 any audience and then a second time either in private again or with a naïve audience
323 within visual range. We measured two indicators of warning: alarm calling and gaze
324 marking. We found that subjects decreased the production of warning behavior if
325 encountering the threat twice in private (Non-Social Group). By contrast, if subjects were
326 in the presence of uninformed others when encountering the threat a second time (Social
327 Group), they produced comparably higher rates of communicative behavior.

328

329 In the Non-Social Group, alarm calling decreased from 3 of 4 to 1 of 4 alarm calling
330 subjects, whereas in the private-social condition it increased from 2 of 5 to 3 of 5 subjects.
331 Although this change was not statistically significant, the observed changes across
332 conditions were consistent with the hypothesis that while calls may have initially been

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334 arousal driven, since most individuals showed alarm calls on first exposure, the later
335 production of the target behaviors was modulated by the presence of uninformed others.
336 This interpretation aligns with the finding of Girard-Buttoz et al. (2020) who found
337 chimpanzees were more likely to produce alarm calls in response to predator models
338 when they had not yet heard an alarm call from a conspecific. Given that the animals
339 tested in the pilot showed consistent alarm behavior in response to the decoy spider, it is
340 unlikely that the lack of group differences in warning behavior reflected a categorization
341 of the target stimulus as irrelevant or non-threatening. Instead, we suggest that alarm
342 calling may have required additional experience with the stimulus to be communicated
343 about.

344
345 Indeed, in another study using a similar approach, older chimpanzee individuals were
346 more likely to produce alarm calls in response to the stimulus while gazing behaviors
347 (measured through gaze alternations) were common at all ages (Dezecache et al., 2019).
348 These findings suggest that, in contrast to several monkey species wherein juveniles but
349 not adults show alarm responses to novel predators (Leon et al., 2022; Mohr et al., 2023),
350 reliable alarm calling behavior in chimpanzees requires more extensive prior experience
351 of danger, while gazing behavior may not. Moreover, we believe our findings point towards
352 the involvement of other cognitive mechanisms such as the formation of long-term
353 memories on a single-trial basis, since effects were observed at least 10 days after a
354 single experience of the novel stimulus.

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356 Changes in looking behavior were instead significant, being higher in the second trial in
357 the social compared to non-social condition. Gaze is indeed known to play an important

358 role in primate communication. In a study of young chimpanzees in response to a novel
359 threatening model, gaze alternations were consistently observed to co-occur during alarm
360 calling (Dezecache et al., 2019). Similar patterns have been observed in response to more
361 familiar predators and are commonly interpreted as fulfilling a 'marking' function that
362 allows conspecifics to locate danger (Crockford et al., 2017; Schel et al., 2013). We could
363 not measure gaze alternations in this study because in the non-social condition there
364 would be no social partner to gaze towards, creating a bias between conditions. It
365 nonetheless seems plausible that the gaze behavior observed in the social condition also
366 fulfilled a communicative function, consistent with a motivation to inform uninformed
367 conspecifics by drawing their attention to potential threats via sustained looking to the
368 visual referent.

369
370 This said, we concede that the evidence presented here is provisional and open to
371 competing interpretations: for instance, it remains possible that individuals produced more
372 looking behavior towards the decoy spider in the presence of conspecifics because of the
373 increased arousal of the focal individual due to the mere presence of others or in light of
374 the potential threat that the spider may have represented for other group members. These
375 alternative explanations cannot be presently ruled out insofar as the first encounter with
376 the stimulus was always asocial. To test for such confounds, further experimental work
377 could present individuals with the stimulus on first encounter in the presence of
378 conspecifics. If individuals are motivated to inform others, we would expect
379 communicative behaviors to not increase in the second trial if the signalers have evidence
380 that the potential audience was already knowledgeable about the about the threat.

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385 One important methodological limitation in the present study is the lack of randomization
386 in group assignment: individuals that we encountered alone were opportunistically
387 included in the Non-Social group. According to the STRANGE framework (Webster &
388 Rutz, 2020), this may give rise to a self-selecting bias: perhaps individuals in the Non-
389 Social group were more likely to be found alone because less inclined to socialize with
390 others. This is a crucial confounding factor, insofar as individuals who are disposed to be
391 less social may also be less motivated to inform others. Buttressing this possibility, it has
392 been recently shown that more sociable chimpanzees are more persistent in their gestural
393 communication (Roberts & Roberts, 2019). Tempering the worry that self-selection biases
394 might explain the observed pattern, individuals in each group produced consistent and
395 comparable alarm responses to the stimulus during the pilot phase. For this reason, self-
396 selecting bias between experimental conditions is unlikely to explain the observed
397 patterns.

398

399 **CONCLUSIONS**

400 To conclude, in the present study we aimed to examine whether chimpanzee produced
401 alarm calls and gaze marking to inform others when already familiar, and thus plausibly
402 no longer aroused, by the relevant stimulus. While further experimental work remains to
403 be done in order to provide stronger evidence of this motivation in chimpanzees, our
404 research represents an important first step, as it introduces an original and potentially
405 fruitful field research protocol and provides further support to the claim that chimpanzee
406 communication is driven by the motivation to inform others.

407

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