EVOLUTIONARY BIOLOGY

Vocalizing in chimpanzees is influenced by social-cognitive processes

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Adjusting communication to take into account information available to one's audience is routine in humans but is assumed absent in other animals, representing a recent development on the lineage leading to humans. This assumption may be premature. Recent studies show changes in primate alarm signaling to threats according to the receivers' risk. However, a classic problem in these and other perspective-taking studies is discerning whether signalers understand the receivers' mental states or simply are responding to their behavior. We designed experiments to exclude concurrent reading of the receivers' behavior by simulating receivers using prerecorded calls of other group members. Specifically, we tested whether wild chimpanzees emitted differing signals in response to a snake model when simulated receivers previously emitted either snake-related calls (indicating knowledge) or acoustically similar non–snake-related calls (indicating ignorance). Signalers showed more vocal and nonvocal signaling and receiver-directed monitoring when simulated receivers had emitted non–snake-related calls. Results were not explained by signaler arousal nor by receiver identity. We conclude that chimpanzees are aware enough of another's perspective to target information toward ignorant group members, suggesting that the integration of signaling and social cognition systems was already emerging in early hominoid lineages before the advent of more language-specific features, such as syntax.

INTRODUCTION

A major question in science is when in evolutionary history did animal communication become influenced by another's rather than one's own perspective or knowledge (*1*–*6*). Some primate alarm calling is influenced by the receivers' behavior, such that signalers appear to modify their alarm calling according to the receivers' level of risk in the face of a threat. Harem male monkeys, for example, alarm call more when group members are close to a threat [*Cercopithecus mitis* (*7*)] and stop calling only after group members have also alarm called [*Presbytis thomasi* (*8*)]. Chimpanzees are more likely to call when group members have not seen the threat (*9*, *10*) or not heard threat-related calls (*9*) and are more likely to stop alarm calling after others have climbed to safety (*10*). Previous studies suggest that signalers may take into account the perspective of receivers with respect to a current threat when signaling. We call this the "receiver knowledge hypothesis." However, previous studies (*7*–*10*) do not rule out the possibility that signalers simply change their signaling after reading the receivers' behavior in threat contexts (approaching, climbing, or behavior associated with alarm calling) rather than because of what receivers could see or know. A classic problem in these and other perspective-taking or mind-reading studies is finding an experimental paradigm that convincingly excludes the possibility of concurrent behavioral cueing, which could enable signalers to predict the receivers' subsequent behavior through simpler mechanisms such as associative learning rather than requiring mental state attribution (*5*, *6*).

Some studies have examined the influence of perspective-taking on vocal signaling in food rather than alarm contexts. In these studies, chimpanzees changed their signaling depending on whether they could be seen by a human experimenter with access to food (*11*, *12*). Chimpanzees called more when the human experimenter had his or her back turned or eyes closed rather than when facing chimpanzees with his or her eyes open. In contrast, chimpanzees gestured more when the human experimenter faced them or had his or her eyes open. In addition, they changed the vocalization emitted depending on whether a human might facilitate food retrieval (*13*). When only food was present, chimpanzees emitted food grunts. When a human stood next to the food, chimpanzees emitted attention-getting vocalizations. Together, these studies indicate that chimpanzees change their vocal production depending on the attentional state of the human receiver with respect to themselves, in contexts where they can gain a food reward. Motivation to vocalize could either take into account another's perspective or be based on associative learning processes. Further research is required to determine the extent to which social cognition might influence vocal production.

Here, we examine whether chimpanzee vocal production is influenced by another's perspective in the context of threat. We present two studies. Experiment 1 is a new analysis of nonvocal behavior, drawn from a previous experiment that focused exclusively on vocalizations, to assess what aspects of receiver behavior signalers attend to. Experiment 2 excludes the possibility of reading the receiver's behavior besides the vocalization presented, by using calls played back through a loud speaker to simulate receiver presence. The experiment contrasts conditions in which receivers are apparently aware or unaware of a threat, through information expressed only in the playback vocalization. Some seconds after hearing the playback, subjects then see a snake model, and without presenting further receiver behavior, we examine any subsequent changes in the subjects' vocal output and speaker-directed attention.

The receiver knowledge hypothesis predicts that in the presence of threats—here, snakes—chimpanzees motivated to inform ignorant rather than knowledgeable others would invest more in signaling and monitoring receivers when receivers had not seen the snake or emitted snake-related calls. The hypothesis also predicts that the signaling effort drops once the receivers express awareness of the snake, by either looking at the snake in experiment 1 (Fig. 1) or by emitting snake-related alarm calls in experiment 2 (Fig. 2). Thus, each experiment required subjects to

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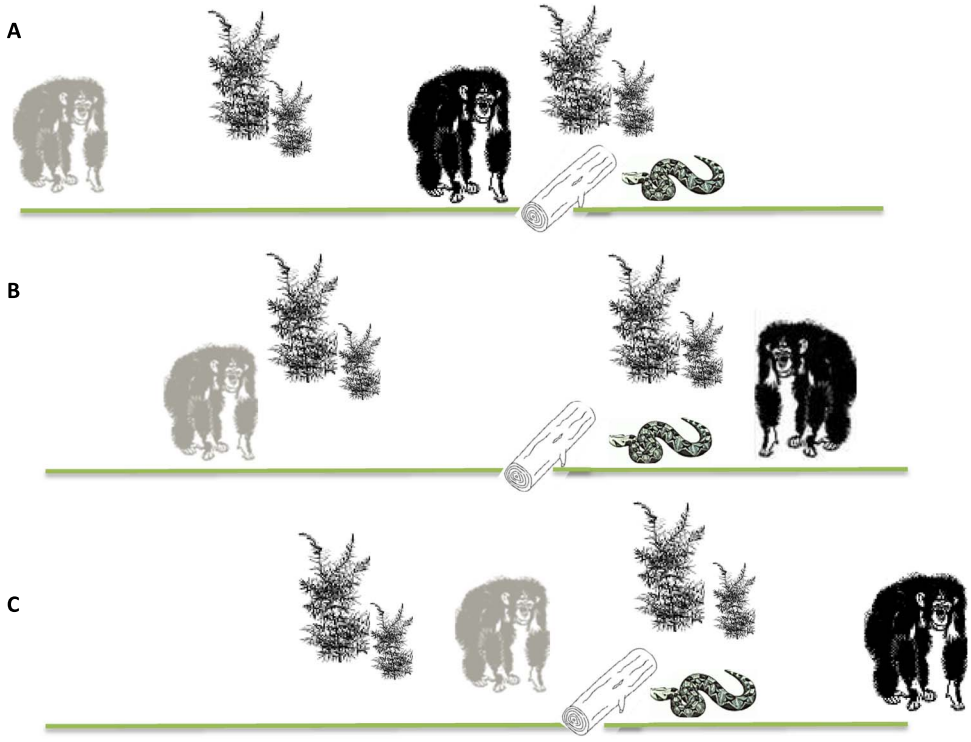

Fig. 1. Experiment 1 setup and predictions: Chimpanzee behavior while seeing a snake model. We placed a partially hidden snake model (fig. S1) along the anticipated travel path of a subject. We tested whether marking behavior took the visual perspective of receivers into account (whether the receiver could see a snake model). Black chimpanzee, subject's position and orientation with respect to the snake model and receivers; gray chimpanzee, the receiver's position and orientation. Behavior of the subjects upon seeing the snake when both arrive from the left side: (**A**) Subject's attention is snake-focused. (**B**) Marking, strictly defined as repositioning oneself to have direct visual access to both the snake and the receiver and to alternate gaze between the snake and the receiver. Gaze alternation was defined as head-turning between the receiver and the snake without intervening looks in other directions. Receivers were defined as having seen the snake once they had an unobstructed view to the model. (**C**) The subject leaves the snake. Predictions: H1 (receiver knowledge), the subjects engage in an initial phase of (A) but rapidly switch to (B). The subjects only switch from (B) to (C) once the subjects have seen that the receivers see the snake. H2 (signaler habituation), the subjects engage in (A) and (C) only. H3 (receiver identity), the subjects are more likely to engage in (B) if at least one receiver is a bond partner. H4 (receiver behavior), the subjects are more likely to stop engaging in (B) when the subjects see that the receivers are no longer at risk, such as when leaving the snake. Green line, trail; log, hiding snake model; snake model, gaboon or rhinoceros viper.

monitor the receivers' awareness of snakes in a different modality: visually in experiment 1 and auditorily in experiment 2.

We tested the receiver knowledge hypothesis (H1) within the context of three alternative, not mutually exclusive hypotheses. The signaler habituation hypothesis (H2) predicts that, during each trial regardless of nearby receivers, signalers with, rather than without, previous exposure to the snake (seeing the snake or hearing snake-related calls) (*14*, *15*) will be less aroused upon seeing the stimulus and will have a shorter overall reaction due to a simple habituation effect (*14*–*19*). The receiver identity hypothesis (H3) predicts that alarm calling is influenced by the subjects' relationship with the receiver, because previous studies (*9*, *10*, *20*) show that signalers alarm call more when receivers are bond partners. The receiver behavior hypothesis (H4) predicts that alarm call production is driven by the signaler monitoring the risk behavior of receivers, such as approaching the snake (*10*, *21*), rather than monitoring the information available to receivers. In this case, signalers should stop signaling once the risk to receivers is reduced, such as when they leave the snake rather than when they approach or sit in closest proximity to the snake.

Most snakes are only dangerous to chimpanzees until detected (*22*), after which they cease to be a threat. Hence, informing group members of the presence of snakes could function to bring group members into a position of safety. Chimpanzees produce both quiet ("alert hoos") and loud ("alarm barks") alarm calls to snakes in ways that suggest an underlying intention to change another's behavior [sensu Dennett (*23*)]. When they produce such calls, they typically look back and forth between the snake and the receiver and persist in both of these behaviors until the apparent goal has been achieved (*10*, *24*, *25*). Gaze alternation and persistence in signaling until the goal has been met have long been used as operational definitions of intentional communication in both developmental psychology and ape research (*25*–*27*).

Alert hoos are produced in response to serious threats, like snakes (*9*), and they direct the receivers' attention to the general vicinity of the snake (*28*). However, further cues are likely required to locate these highly camouflaged snakes (see fig. S1 and video S1), such as following the gaze of signalers (*28*), a widespread capacity among primates (*29*). Chimpanzees can show sentinel-like behavior (*9*, *10*, *28*), sometimes appearing to wait next to a snake as if to "mark" the position of the hidden threat for others (Fig. 1 and video S1). Marking, in addition to alert hoos, potentially assists receivers in locating camouflaged snakes. To test whether marking was influenced by receiver presence or behavior, we determined whether the onset and cessation of marking behavior were influenced by whether receivers could see the snake (H1, receiver knowledge) or by the three alternative explanations (H2, signaler

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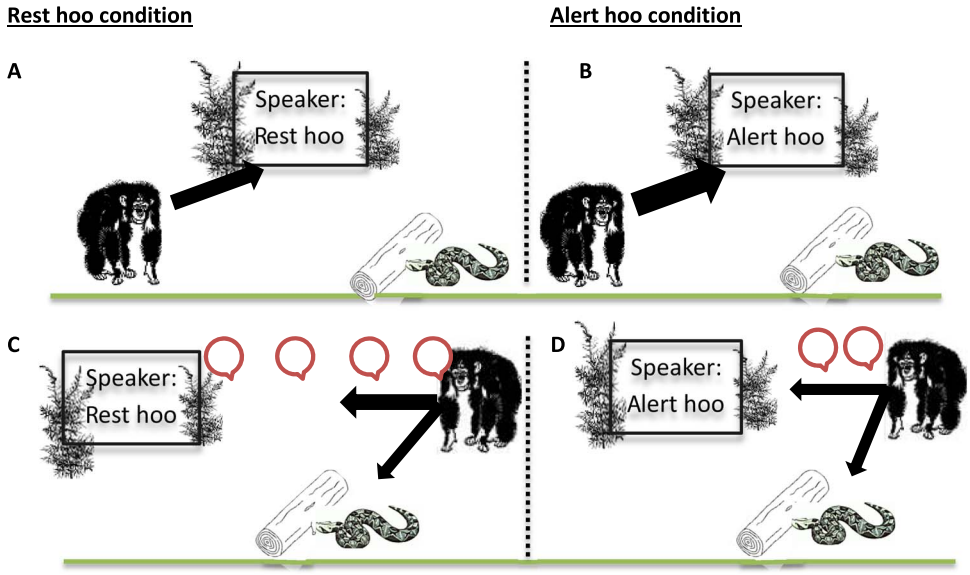

Fig. 2. Experiment 2 setup and illustration of the results: A two-stimulus design where chimpanzees first hear a playback and then see a snake model. Arrow thickness indicates chimpanzees' level of attention. Speak bubbles represent number of calls and rate of calling. (**A** and **B**) Presentation of stimulus 1. (**C** and **D**) Presentation of stimulus 2. The subject walks along a path and hears a playback of either a rest hoo (A) or an alert hoo (B), simulating a receiver. The subjects hearing a threat-related call (an alert hoo) looked more to the speaker than after hearing a rest hoo, a call not associated with threats. After reacting to the speaker, the subjects then continued walking and then saw a snake model hidden behind a log, some seconds after hearing the playback of a hoo. No further receiver behavior is presented. We asked: Does the subjects' behavior change upon seeing the snake in a way that is consistent with them monitoring in the receivers' perspective? (C) In the rest hoo condition (receiver-ignorant), consistent with the subjects keeping track of the receivers' perspective, the subjects persisted in monitoring the speaker and were highly likely to call and mark the position of the snake. (D) In contrast, in the alert hoo condition (receiver-knowledgeable), the subjects dropped interest in monitoring the speaker, and called and marked little. Slower calling rate in (C) compared to (D) is better explained by the receiver knowledge than the signaler habituation hypothesis. There was no change in attention given to the snake across conditions. In the absence of visual cues, it appears that the subjects not only monitored the receivers' awareness of a threat but also changed their communication depending on the receivers' awareness of the threat. Green line, trail; box, speaker hidden behind vegetation; snake model, gaboon or rhinoceros viper hidden behind a small log. Relative distances at the time of playback were 5 to 10 m between the subject and the speaker, the subject and the snake, and the speaker and the snake.

habituation; H3, receiver identity; and H4, receiver behavior). We defined the receiver's first sight of the snake as occurring when receivers had the first unobstructed view of the snake and simultaneously showed an interruption of their current behavior, such as pausing while walking. We operationalized "marking" as repositioning oneself to have direct visual access to both the snake and the receiver and as alternating gaze between the snake and the receiver. Given the dense vegetation, we deemed repositioning to be necessary for effective monitoring of receivers with respect to the snake: to enable visibility of both simultaneously (see Fig. 1). Marking onset was the first look toward receivers after repositioning. Marking cessation was when the signaler either left the snake model or engaged in no further gaze alternation. Gaze alternation was defined as head-turning between the receiver and the snake without intervening looks in other directions.

RESULTS

Experiment 1: Snake model placement

Marking is influenced by receivers' awareness of the snake

In experiment 1 (*9*), we placed a snake model (fig. S2) along the anticipated travel path of chimpanzees and videoed their behavior in proximity to the snake model (Fig. 1) (*9*). Previously, we examined the calling behavior of subjects from this data set (*9*), whereas we examined here the nonvocal behavior using a series of generalized linear mixed models (GLMMs) (see Materials and Methods). Marking occurred in 14 of 37 trials (n = 22 chimpanzees). In the first model, subjects were more likely to engage in marking (see Fig. 1) if receivers had not seen the snake and if receivers were bond partners (Table 1A). Whether subjects were the first to see the snake, or receivers were still approaching the snake and hence were approaching danger, did not show significant differences (Table 1, A and B).

It should be noted that, in all cases, whether marking occurred, there was an initial period of exclusively snake-focused attention, where subjects did not look in other directions (table S1). In a second model, examining the relative duration of marking, the subjects marked significantly longer before than after the receivers saw the snake (GLMM: β = 1.07, SE = 0.26, t = 4.15, P = 0.0003; Fig. 3A: mark duration before, mean ± SD = 55 ± 42 s; mark duration after: 15 ± 6.3 s; video S2). When examining cessation of marking, in all cases in which marking occurred, the subjects stopped marking only after the receivers had seen the snake (Fig. 3B). In contrast, cessation in marking did not coincide with the behavior of the receivers that reduced their risk, specifically as the receivers left the snake (only 2 of 14 cases) (Fig. 3B). A small number of trials suggested that cessation of marking occurred more rapidly when receivers also emitted an alert hoo upon seeing the snake: Receivers emitted alert hoos in five trials in which marking occurred. In four of these five cases, signalers stopped marking rapidly, within 5.4 ± 5.7 s (mean ± SD; range, 1 to 14 s; n = 4 subjects). In sum, receivers seeing the snake influenced the occurrence or cessation of marking, rather than the subjects' own exposure to the snake

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Table 1. Experiment 1: Chimpanzee marking behavior at snake models with respect to receivers. (A and B) The likelihood of subjects to initiate marking. (C) The impact of signal type on receiver behavior. Binomial GLMMs: Marking, reposition oneself to see both the snake and the receiver and gaze alternate between the snake and the receiver. H1, receiver has seen the snake before signaler calls or marks (yes/no); H2, subject is first to see the snake (yes/no); H3, receivers include a bond partner (yes/no); H4, subjects could see or hear receivers approaching when first to see the snake. Random factors include subject identity and event. Bold: $P < 0.05$. Model significance versus null model built of control predictors (for H2 to H4) and random effects: (A) $\chi^2 = 9.91$, df = 1, $P = 0.002$; (B) $\chi^2 = 4.2$, df = 1, $P = 0.038$. $n = 37$ cases, 22 subjects, and 12 snake placement events. We conducted two models instead of one due to model stability issues with four predictor variables. After running model (A), we removed the nonsignificant variable, replaced it with the remaining predictor variable, and reran the model [model (B)]. All significant variables remain significant with a Bonferroni correction [required across models (A) and (B)]. Model (C) included only receivers who had not seen the snake. $n = 27$ cases, 17 subjects, and 12 events: $\chi^2 = 6.41$, df = 1, $P = 0.011$. See table S1 for the source data.

Predictor variable	β	SE	χ^2	*P*
A. Response variable: mark (yes)				
Intercept	11.60	9.80		
H1: Receiver knowledge: receiver has seen the snake (no)	**21.34**	**10.4**	**9.91**	**0.002**
H2: Habituation: subject is first to see the snake (yes)	−1.77	5.70	0.07	0.70
H3: Receiver identity: bond partner present (yes)	**19.98**	**8.13**	**11.60**	**0.001**
B. Response variable: mark (yes)				
Intercept	**10.76**	**7.20**		
H1: Receiver knowledge: receiver has seen the snake (no)	**19.13**	**7.20**	**4.28**	**0.008**
H3: Receiver identity: **bond partner present (yes)**	**20.48**	**8.98**	**13.45**	**0.022**
H4: Receiver behavior: receivers approaching (yes)	2.01	5.72	0.14	0.73
C. Response variable: receiver behavior cautious approach (yes)				
Intercept	0.41	0.91		
Mark and call (yes)	**2.60**	**1.13**	**6.44**	**0.011**
Call (yes)	−0.69	1.22	0.32	0.57

(Table 1A) or other aspects of receiver behavior, such as whether receivers were in the process of approaching the snake (Fig. 3B and Table 1B).

Receivers use alarm calling and marking behavior to locate snakes

In a third model, receiver behavior varied depending on the subjects' signaling, with receivers being more likely to see the snake when both signals (calling and marking) were given rather than just calling or no signal (GLMM: $\chi^2 = 6.41$, df = 1, $P = 0.011$; Fig. 3C and Table 1C). Specifically, receivers were more likely to cautiously approach rather than avoid the snake in the 12 trials when marking by signalers co-occurred with calling (cautious approach, 10 of 12 trials; table S1 and video S2) compared to when calling occurred alone (cautious approach, 2 of 8 trials; video S3). Signaling ensured greater safety for receivers in that when subjects signaled, whether calling or marking (22 trails), receivers never passed within 1 m (biting distance) of the snake (Fig. 3C and table S1). In contrast, in 40% (6 of 15) of trials, when subjects gave no signal, receivers passed within biting distance (1 m) of the snake, apparently unaware of the snake's presence. Given that marking behavior showed signs of being highly receiver-sensitive, we included it as a key variable in experiment 2.

Experiment 2: Simulation of chimpanzee receiver

Signaling at snakes is influenced by a simulated receiver's previous vocalization

In a second experiment (Fig. 2), as chimpanzees walked down a path, we played a call from a hidden speaker, simulating the presence of another chimpanzee. After reacting to the playback, the subjects continued to walk down the path for a further 5 to 10 m. The subjects then saw a second stimulus, a previously placed snake model hidden behind a log (fig. S1), some seconds after hearing the playback. We tested whether the subjects' reaction to the snake changed depending on the call type they had heard some seconds earlier. No further cues representing the simulated chimpanzee (the receiver) were presented. Using a within-subjects design, we aimed to expose subjects to two trials counterbalanced for call type so that subjects were played either a "rest" hoo or one to three "alert" hoos. We tested the receiver knowledge (H1) and signaler habituation (H2) hypotheses and controlled for receiver identity (H3) and receiver behavior (H4) in the experimental design. The subjects' vocal and nonvocal behaviors upon seeing the snake differed depending on the call type they had heard some seconds earlier [permutation test correcting for multiple testing (*30*): $\chi^2 = 62.47$, $P = 0.004$, $n = 10$ subjects; Fig. 4 and Table 2]. The pattern of behaviors mainly

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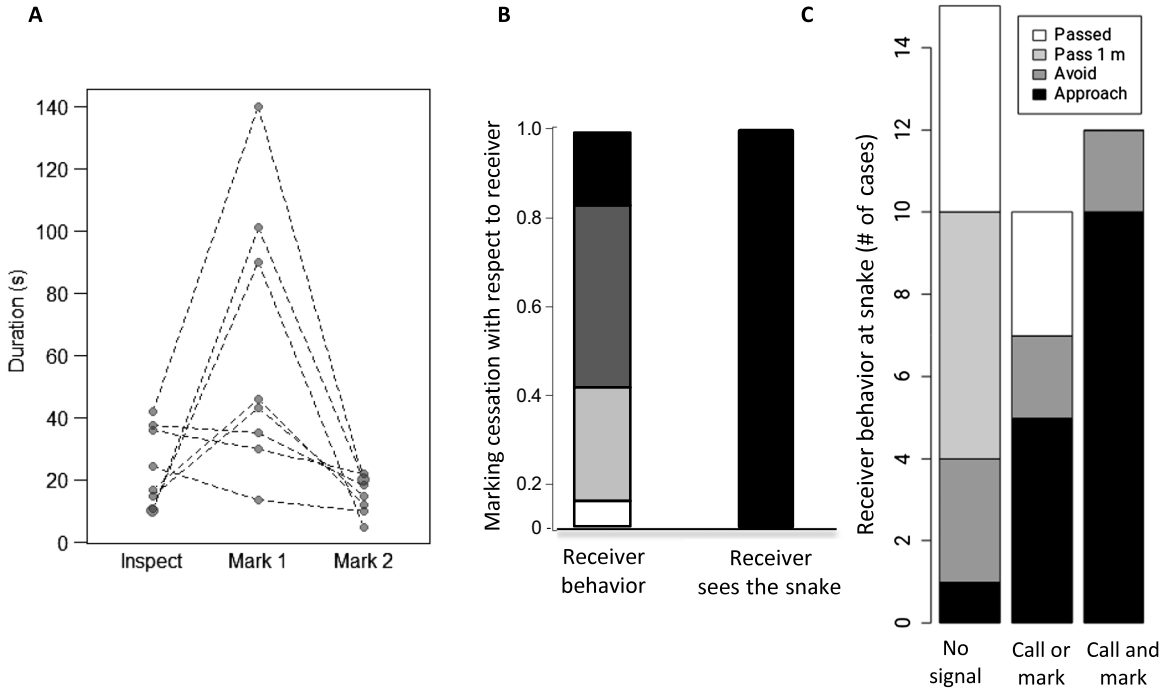

Fig. 3. Experiment 1: Subjects' marking at a snake model is influenced by the receivers' perspective and influences receivers' responses. (**A**) Relative duration of the subjects' marking: before (mark 1) and after (mark 2) receivers have seen the snake. Dots joined by dashed lines, data per subject averaged across trials. Mark 1 + mark 2 = total marking time. Inspect, duration over which the subjects' attention remains snake-focused before engaging in marking (mean ± SD, 24 ± 13 s; range, 10 to 46 s; marking defined in Fig. 1). Mark 1, duration from the beginning of marking until the receiver sees the snake (mean ± SD, 55 ± 42 s; range, 7 to 140 s). Mark 2, duration over which marking continues after the receiver has seen the snake until the subject leaves snake or no longer looks to the snake (mean ± SD, 15 ± 6.3 s; range, 4 to 22 s). Darker dots, more data points per value. *$P < 0.05$, ***$P \leq 0.001$. Model significance versus the null model: $\chi^2 = 12.99$, df = 2, $P = 0.002$, $n = 8$ subjects, 10 cases, and 7 events. GLMM estimates: inspect versus mark 1: $\beta = 0.58$, SE = 0.26, $t = 2.25$, $P = 0.03$; mark 2 versus mark 1: $\beta = 1.07$, SE = 0.26, $t = 4.15$, $P = 0.0003$; inspect versus mark 2: $\beta = -0.49$, SE = 0.26, $t = -1.89$, $P = 0.067$. (**B**) Marking cessation with respect to receiver behavior (first bar) or when receiver sees the snake (second bar); *y* axis, proportion of cases. The bars show the subjects that stopped marking after witnessing the following receiver behavior: left bar (risk-reducing behavior): white, leave the snake (not risk-reducing behavior); light gray, still approaching the snake; dark gray, closest approach to the snake; black, no movement during marking; right bar: black, subjects stop marking after receiver sees the snake; 14 cases from $n = 10$ subjects (8 events). (**C**) The receivers' behavior toward the snake depends on the subjects' signaling. $n = 37$ cases, 22 subjects (12 events). Table 1C shows the test result. Three bars show the differential signaling of subjects: no signal, call or mark (calling, $n = 8$; marking, $n = 2$), and call and mark. Blocks of color indicate different receiver behaviors with respect to the snake model after the subjects' signaling behavior. Approach, cautious approach to see a snake model; avoid, a detour of >5 m around the snake; pass 1 m, pass within the biting range of snake model—apparently unaware of the snake; passed, receiver had either already passed the snake or did not change position while the subject could see the snake model.

supported H1 (receiver knowledge) but not H2 (signaler habituation). Specifically, the subjects emitted more alert hoos after hearing a rest hoo (not associated with snakes and thus indicating that the receiver is not aware of the snake) rather than an alert hoo (associated with snakes and thus indicating that the receiver is aware of the snake) (Fig. 4A and Table 2). Note that, similar to the study by Crockford *et al.* (*9*), the subjects never emitted alert hoos until they had seen the snake. The subjects were also more likely to engage in speaker-directed marking and to combine marking and calling after hearing rest hoos rather than alert hoos (Fig. 4D, Table 2, and videos S4 and S5). Speaker-directed monitoring, after compared to before seeing the snake, dropped in the alert hoo condition but persisted in the rest hoo condition (Fig. 4F and Table 2).

Against the signaler habituation (H2) hypothesis, the subjects' rate of alert hoo production was slower, and the latency to the first call tended to be slower in the rest hoo condition rather than in the alert hoo condition (Fig. 4, B and C, and Table 2; see Materials and Methods). There was also no significant effect on the number of alert hoos played (whether one or three hoos) on the subjects' own likelihood of emitting an alert hoo, and there was no effect across conditions on the duration that subjects looked at the snake (Table 2).

Speaker-directed marking and calling were not significantly influenced by possible confounding factors, the relative dominance rank of subjects compared to simulated receivers, and the latency from playback to seeing the snake (table S4), nor whether subjects were alone or traveling with a maximum of two others when hearing the playback (Table 2). The one exception was that the presence of other chimpanzees was associated with a tendency for slower rates of calling across conditions.

DISCUSSION

Two different experiments have revealed that chimpanzee vocal and nonvocal responses at snakes are modified according to the receivers' relation to a current threat. In experiment 1, in one-third of cases, usually when bond partners were present, the signalers marked the location of the snake model, alternating gaze between the receivers and the snake model (hereafter, snake). Signaling provided greater safety and

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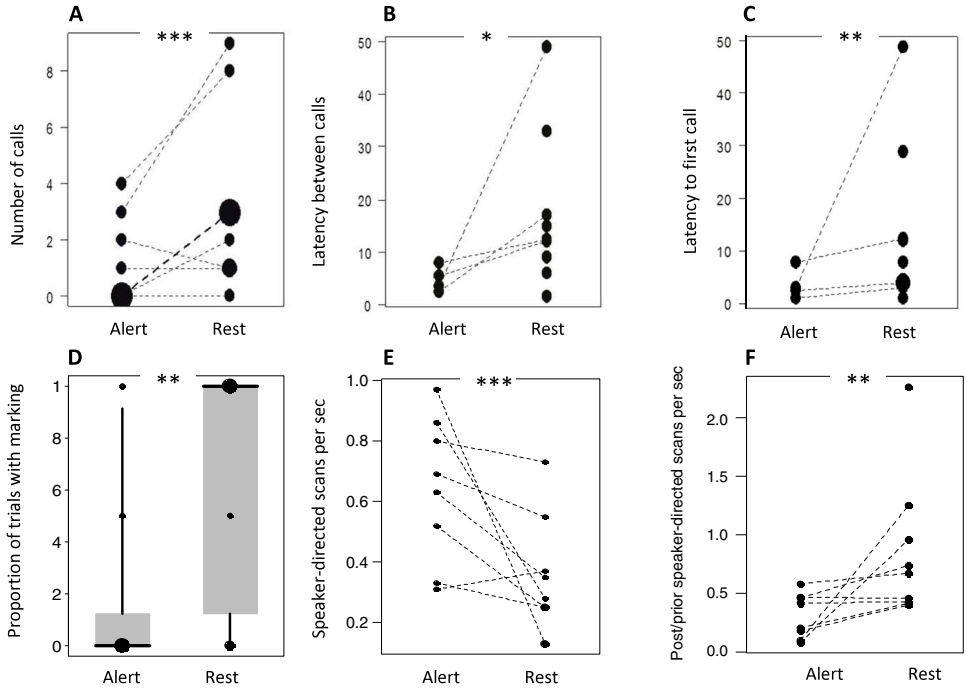

Fig. 4. Experiment 2: Subject's signaling behavior toward the snake model differed depending on experimental conditions—the playback stimulus heard previously. (**A** to **D**) Comparison of response to alert versus rest hoo stimulus. Dots joined by dashed lines, data per subject averaged across trials within conditions. Larger dots, more data points per value. *$P < 0.1$, **$P < 0.05$, ***$P < 0.01$. Bar plot shows mean + SD with 95% confidence interval. GLMM results are shown in Table 2. $n = 10$ subjects, 21 trials, and 12 dyads. Note that sample sizes and thus statistical power in (B) and (C) are particularly small, because only cases where calling occurred could be included; *x* axis, experimental condition (playback stimulus played). (**E**) Speaker-directed scans after the playback before seeing the snake. (**F**) Post/prior speaker-directed scans comparing subjects' scans after seeing the snake with those before seeing the snake.

more threat-related information for the receivers. When no signals were given, the receivers passed within biting distance of the snake in 40% of cases. When only alert hoos were given, the receivers avoided the snake in 75% of cases. When marking also occurred, the receivers were more likely to cautiously approach rather than avoid the snake. It seems that although alert hoos advertise the general location of a hidden threat, marking points out the precise location, enabling others within visibility of the signaler to gaze-follow and to safely detect the hidden threat (for example, videos S1 and S2).

In experiment 2, after the subjects saw a snake model, they called and marked more toward the speaker when a call not associated with threats was played back some seconds earlier. Strikingly, the subjects also showed a speaker-directed attentional shift from before to after seeing the snake model, rapidly losing interest in the speaker direction in the alert hoo condition but maintaining interest in the speaker direction in the rest hoo condition, although no further receiver behavior was presented. Rest hoos, which typically elicit least speaker-directed attention compared to alert hoos (*28*), elicited greater persistence in attention to the speaker after the subjects had seen the snake. The observed changes in attention within and between conditions are hard to explain in terms of the signalers' arousal state or habituation to the stimulus or in terms of the subjects merely expressing a simultaneous interest in both the speaker and the snake (*31*). Experiment 1 findings also suggest that the latter explanation is unlikely to be the case, because the signalers only stopped marking after the receivers had seen the snake. In addition, in three trials in experiment 1 where the receivers were slow to see the snake, the signalers temporarily stopped attending to the snake, although they remained within sight of the snake. In each case, eventual interest or approach from the receiver toward the snake precipitated the subjects' re-engagement with the snake, until the receiver saw the snake (see video S2 at 2 min 45 s).

In terms of calling behavior in experiment 2, against H2 (signaler habituation), calling was not more rapid in the rest hoo condition compared to the alert hoo condition. Rather, the opposite occurred—the latency to the first hoo and the average latency between calls were significantly longer in the rest hoo condition than in the alert hoo condition (Fig. 4, B and C). Given that receivers were too far away for the snake to represent an urgent threat, signalers may have invested in monitoring receiver activity (H1, receiver knowledge) as much as in calling. To effectively monitor the movements of out-of-sight chimpanzees, individuals need to remain silent and still to listen for audible cues from the other (this is a frequent pattern seen in chimpanzees in their low-visibility habitat, such as when engaged in long-distance contact call exchanges: Individuals may stop traveling to call and then listen, a pattern that may be repeated several times before continuing to travel, personal observation). A simultaneous motivation to both inform and monitor could result in the observed slower rate of calling after hearing a rest hoo rather than an alert hoo.

It should be noted that although more alert hoos were elicited in the rest hoo conditions than in the alert hoo conditions, alert hoos were nonetheless elicited in both conditions. Chimpanzees only extremely rarely emit alarm calls when they cannot see a threat (*9*) and do not alarm call merely in response to another's alarm call, in contrast to forest monkeys (*15*). Thus, alert hoos may be associated not only with a snake but also with a signaler seeing a snake. Our results from experiment 1 suggest that alert hoos occasionally emitted by receivers may function as "confirmation" of having seen the snake. This may have motivated subjects (in the "role" of receivers) to emit an alert hoo upon seeing the

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Table 2. Experiment 2: Subjects' vocal, nonvocal, and monitoring behavior at snake models is best explained by the receiver knowledge, not signaler habituation, hypothesis. Subjects' overall responses across all tests differed significantly across conditions (permutation test correcting for multiple testing: χ^2 = 62.47, P = 0.004). Parentheses denote the variable level that reflects the estimate when tested against the alternative level. GLMMs: H1 (receiver knowledge), supported or tentatively supported by models (B) to (H); H2 (signaler habituation), not supported by models (B) to (H). n = 10 subjects, 21 trials, and 12 dyads. Bold: P < 0.05; italic, P < 0.1. Test predictor for all models, experimental condition (rest hoo and alert hoo). Random factors for all models include subject identity, dyad identity of subject, and call provider. Binomial, models (B), (E), and (F); Gaussian, models (A), (C), (D), and (G) to (I). Model significance versus null model, effect size (marginal R^2): (A) χ^2 = 10.31, df = 1, P = 0.006; R^2 = 0.16; (B) χ^2 = 6.7, df = 1, P = 0.009; (C) χ^2 = 3.12, df = 1, P = 0.077; R^2 = 0.30; (D) χ^2 = 3.96, df = 1, P = 0.046; R^2 = 0.32; (E) variable "alone" excluded due to model stability: χ^2 = 7.89, df = 1, P = 0.005; (F) χ^2 = 9.9, df = 1, P = 0.002; (G) χ^2 = 6.4, df = 1, P = 0.25; R^2 = 0.26; (H) χ^2 = 2.65, df = 1, P = 0.10; R^2 = 0.17; (I) χ^2 = 6.9, df = 1, P = 0.0085; R^2 = 0.41. For models (C) and (D), cases containing zeros were excluded; thus, P values are likely affected by low power (see Fig. 4, C and D, for paired data plots, table S2 for source data, and table S4 for additional analyses of control variables).

Response variable	Predictor variable	β	SE	χ^2	P	H1	H2
Calling and marking behavior							
A. Number of calls emitted*	Intercept	0.62	0.27				
	Condition (rest hoo)	**0.56**	**0.18**	**6.73**	**0.009**	**Yes†**	**Yes†**
	Alone (yes)	0.03	0.38	0.01	0.94		
B. Call or not	Intercept	11.23	8.08				
	Condition (rest hoo)	*15.03*	*10.28*	*3.03*	*0.082*	*(Yes)*	*No*
	Number of alert hoos played	−0.13	2.97	0.002	0.97	—	No
C. Latency to first call*	Intercept	1.66	0.41				
	Condition (rest hoo)	*0.85*	*0.46*	*3.12*	*0.077*	*(Yes)*	*No*
	Alone (yes)	*−0.77*	*0.43*	*2.88*	*0.090*		
D. Median inter-call interval*	Intercept	8.65	5.96				
	Condition (rest hoo)	**12.66**	**6.65**	**3.96**	**0.046**	**Yes**	**No**
	Alone (yes)	−9.12	6.28	2.43	0.12		
E. Call and mark co-occurrence	Intercept	−10.83	6.02				
	Condition (rest hoo)	**20.28**	**8.33**	**7.89**	**0.005**	**Yes**	**No**
F. Mark or not	Intercept	−10.0	5.14				
	Condition (rest hoo)	**20.10**	**7.72**	**9.86**	**0.009**	**Yes**	**No**
	Alone (yes)	−0.26	4.90	0.003	0.96		
Attentional state							
G. Scans to speaker/s: Post/prior seeing the snake	Alone (yes)	0.50	0.20				
	Condition (rest hoo)	**0.46**	**0.16**	**6.42**	**0.011**	**Yes**	**No**
	Alone (yes)	−0.25	0.28	0.77	0.38		
H. Looking duration to the snake before first looking away	Intercept	1.77	0.22				
	Condition (rest hoo)	0.38	0.25	2.65	0.11	**No**	**No**
	Alone (yes)	−0.24	0.25	1.10	0.30		
I. Scans to speaker/s after playback before the snake	Intercept	0.53	0.08	**6.91**	**0.009**		
	Condition (rest hoo)	**−0.26**	**0.08**			—	—
	Alone (yes)	0.17	0.09	2.60	0.107		

*Transformation, log + 1. †Confirms results of previous study but does not discriminate between hypotheses.

snake after they heard a playback of an alert hoo, but this requires further testing.

In sum, subjects engaged in greater signaling and monitoring effort when simulated receivers had not emitted snake-related calls. This result could not have been due to signalers responding to concurrent behavior from receivers related to the playback call, given that there was no additional behavior after the initial played back call. Using a simulated receiver enabled us to keep receiver identity—and

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hence the relationship between signaler and receiver—constant across conditions. Although primate studies show that signaler habituation, receiver identity, and receiver behavior do affect on the subjects' responses to predators or threats (*7–10*, *32*), experiment 2 showed that chimpanzee signaling at snakes is also apparently driven by the subjects' monitoring of the receivers' current relation to a snake. This is a not a spatially driven relation because receiver proximity to the snake was held constant across conditions. The results mainly supported H1 (receiver knowledge) and not H2 (signaler habituation), suggesting that signaler arousal and habituation to the snake stimulus had a weaker influence on the subjects' behavior than the information expressed by the receivers about a threat or the receiver's perspective with respect to a threat.

We excluded some additional explanations. Given that alarm calls can also function as a recruitment call for predator mobbing purposes in some species, we excluded the influence of mobbing behavior in our experimental design by selecting a stimulus that rarely elicits mobbing —a nonpredatory snake (see the Supplementary Materials). In addition, subgroup size (receivers within earshot) (*21*) cannot explain our results, given that we kept subgroup sizes to a maximum of three individuals including the subject and controlled for the influence of these individuals on signaler response patterns in statistical models.

Bringing together the results from both experiments, the two experiments elicited consistent signaling and receiver-directed behavior from the subjects, specifically increased marking and calling at snakes when the receivers expressed less information about the snake. This was the case although the subjects had access to different receiver behaviors in each experiment. In experiment 1, calling and marking were more likely when the receivers had not seen the snake model. In experiment 2, calling and marking were more likely when the receivers had not heard a snake-related call. The subjects' behavior was generalized irrespective of the modality in which receiver ignorance was presented, suggesting central cognitive processing (*33*) of the relationship between the snake, the receivers, and the receivers' status with respect to the snake. In experiment 1, marking stopped soon after the receivers saw the snake. Unlike in previous experiments where subjects try to attain a personal gain, such as a food item (*5*, *34*), the apparent goal of the subjects was simply that the receivers see the snake, with no immediate personal gain. A possible motivation for this was that once the receivers had seen the snake, the snake ceased to be a threat to the receivers, given the sedentary and likely nonpredatory nature of these snakes to chimpanzees, bringing receivers into a position of safety (*22*).

We cannot completely rule out "killjoy" explanations (*35*), such as that subjects could be behaving on the basis of learned associations between the presence of a snake and the behavior of others, although these experiments make this possibility less likely. For example, in experiment 2, it could be that chimpanzees behave differently when they are the first to see the snake [although here (Table 1A) and previously (*9*), we find little support for this]. Previously, an analysis explicitly only including subjects who were not the first to see the snake likewise found that the subjects' calling behavior varied depending on the information available to receivers (*9*). In addition, previous studies (*9*, *10*) have shown that when new receivers arrive at the snake, subjects increase their rate of calling.

Perhaps a more plausible alternative is that in the presence of a snake, subjects perceive receivers who have neither seen the snake nor emitted snake-related calls as being under threat. It may be this perception, rather than perspective-taking processes, that precipitates subjects' informing and receiver-monitoring behavior. In this scenario, given that the threat faced by the receiver is not directly perceivable (given that there is no receiver nor further presentation of receiver behavior), we suggest that cognitive processing is still required to determine that another individual faces a threat because they have not visually or vocally "engaged" with a third entity, a snake. Here, in a situation from which subjects do not receive any apparent immediate gain (such as a food reward), they apparently invest in monitoring the threat faced by another, even when the threat is spatially (5 to 7 m) and temporarily (mean ± SD, 25.9 ± 21.1 s) separated from the simulated receiver. Together, this indicates that social-cognitive processing is influencing signaling behavior.

Overall, the results suggest that chimpanzee social cognition is not only supported by concurrent behavior reading. Bugnyar *et al.* (*34*) recently reached a similar conclusion for a playback experiment with ravens (*Corvus corax*). They used a playback of sounds of raven movement to indicate receiver presence in a competitive food-caching context. The results indicated that ravens took into account visual access of receivers, indicated by a peephole, even when no receivers could be seen. Bugnyar *et al.* (*34*) concluded that "reduced" theories of mind, such as a "minimal" theory of mind (*36*) or Whiten's "intervening" variable (*37*), provided closer explanations of the subjects' observed behavior than of concurrent behavior reading or of "full-blown" theory of mind (*5*). A more recent study using an anticipatory looking paradigm in chimpanzees indicates that they, like small children, use implicit theory of mind to solve false belief tasks (*38*). In other perspective-taking tasks, chimpanzees can infer the target of another's attention, behave strategically depending on what another can and cannot see (*39*, *40*), and show anticipation of another's goal-directed action in situations where there is no direct gain from doing so (*38*). However, perspective-taking is a complex topic. Whether one individual understands that another seeing an object—or giving a call highly associated with an object—indicates another's current knowledge and hence demonstrates mental state attribution is much debated (*5*, *6*) and will not be resolved here.

Nonetheless, it seems relevant that we consider this body of work when interpreting the results of this study. Here, chimpanzee subjects' signaling and receiver-directed monitoring in both experiments are consistent with the hypothesis that subjects were not only motivated by their own perspective but also took the receivers' perspective with regard to the threat into account. When determining whether this constitutes mental state attribution, minimal theory of mind (*36*), or, more simply, an awareness of the receiver's status with respect to the snake and associated threat level, the cross-modal nature of the receiver behavior available to the subjects in this study will need to be taken into account in further debates on this topic (*6*).

In addition to the social cognition involved in our two experiments, we are also interested in the impact of social cognition on signaling. Although perspective-taking has rarely been shown to influence vocal communication (*3*), apes are more likely to gesture when they can be seen by the receiver (*11*, *13*, *24*) and to vocalize when they cannot be seen by the receiver (*11*, *13*). Here, subjects changed their signaling and receiver-directed behavior depending on the relationship between the snake, the receiver, and the receiver's status with respect to the snake, which was either explicitly visible (experiment 1) or inferred from a vocalization that subjects heard before they had seen the snake (experiment 2).

Thus, it seems highly likely that vocal production depends on social-cognitive processes rather than being entirely emotionally driven (*6*). In a recent review, Fischer and Price (*31*) suggest that primate vocal

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communication is goal-directed rather than limited to the expression of emotional states, although it is not yet clear what social cognition this would entail. Comparative studies are required to examine other species' signaling behavior using comparable experiments to determine the extent to which social cognition influences vocal production. These experiments would be of particular interest in primate species that have already indicated that alarm calling is influenced by a complex relationship between the threat and the receivers, such as has been shown in two primate species with a harem-male social structure (*7*, *8*).

Our results support those of previous studies (*41*, *42*) with captive chimpanzees, which demonstrated that chimpanzees use a gestural point more to human caregivers who are unaware compared to those who are aware of the location of an item (a tool or food) to request the item, although this pointing gesture is not typically seen in the natural gestural repertoire of this species. The pointing aided retrieval of food for the ape subjects; however, Zimmermann *et al.* (*41*) questioned whether the apes would have pointed in the absence of an immediate food reward. In our study, informing ignorant others of a snake offered no immediate benefit for signalers. Studies on language-trained apes have shown informative pointing in the absence of immediate food rewards (*43*). However, it has remained unclear whether these communicative abilities are natural to chimpanzees or are limited to chimpanzees trained by humans (*3*).

In a natural context, it seems that chimpanzees' vocal, nonvocal, and monitoring behaviors at snake models are influenced by social-cognitive processes that are not limited to concurrent behavior reading to an extent not yet demonstrated within the natural communication of nonhuman animals. Here, we show a function of communication in nonhuman animals, which seems to go beyond expressing own current motivations, desires, or needs and suggests a motivation to inform others who have not seen a threat or emitted threat calls. Although this certainly falls short of humans' avid capacity to share thoughts and feelings, this shows initial awareness of what information might be needed and relevant for another, relevance being a central feature of human language usage (*4*, *44*). We demonstrate that chimpanzees likely have a key motivation for developing complex communication, previously thought to be absent in all natural nonhuman communication—to fill another's need for information. This is despite chimpanzees apparently having a limited vocal repertoire and combinatorial capacity, which likely restricts message complexity (*20*, *28*). For the evolution of language, this study suggests that the required cognitive capacities for honing informing in situations when others need the information were to, some extent, in place in our last common ancestor shared with chimpanzees, more than 8 million years ago (*45*). This capacity to integrate communication and social cognition systems is a possible foundation of language evolution, arising before the advent of more language-specific features, such as recursive syntactic structure.

MATERIALS AND METHODS

Animal ethics

Our study was approved by the St. Andrew's Psychology Department Ethics Board and complies with the ethics of both the Institutional Animal Care and Use Committee and the Max Planck Society and the ethics policy of the Department of Primatology, Max Planck Institute for Evolutionary Anthropology (www.eva.mpg.de/primat/ethical-guidelines.html).

Study site and subjects

Subjects were wild-living chimpanzees of the Sonso community in Budongo Forest (*Pan troglodytes schweinfurtii*) (*46*), Uganda, habituated to human observers since 1995. Of a total of 77 chimpanzees, we tested 22 subjects in experiment 1 with a snake model [8 adult males (>15 years), 2 subadult males (10 to 15 years), 7 adult females (>14 years), and 5 subadult females (10 to 14 years)]. Chimpanzees were tested opportunistically, depending on who arrived at the snake (table S1). In experiment 2, we tested 10 subjects using a playback and the snake model placement experiment (5 adult males, 2 subadult males, 2 adult females, and 1 subadult female). Using a within-subjects design, we aimed to test each subject in each experimental condition (table S2). We selected subjects based on their travel habits, choosing individuals that most commonly traveled in central parts of the territory so that multiple trials would be possible in the area where travel paths were easiest to predict (fig. S1; see tables S1 and S2 for source data).

Experiment 1: Snake model placement

We analyzed data from a previously published experiment (*9*) where chimpanzees saw a snake model placed on the anticipated travel trail. Experiments were conducted from October 2008 to July 2010. Necessary criteria for inclusion were that both the subject and the receivers were either visible on video or continuously observed during the trial, resulting in 37 cases of 22 chimpanzees from 12 separate snake placement events (see the Supplementary Materials for variables measured).

Experimental setup. We placed a snake model along the anticipated travel path of a subject (Fig. 1) (*9*). We used partially hidden placement so that the snake would not be visible for more than a distance of 5 to 10 m (videos S2 and S3) but that at least one chimpanzee would be likely to find the snake. We filmed chimpanzees as they approached and saw the snake and continued filming until chimpanzees moved out of sight of the snake or continued with other behavior, such as feeding. Although we aimed to film all the chimpanzees in a given subgroup, this was not always possible due to vegetation. In 4 of 14 marking cases, coding when receivers could see the snake was not visible on video and hence was excluded from relevant analyses (Fig. 3, A and B). Two to four human observers were stationed within 50 m of the snake. They monitored chimpanzees within earshot (<50 m) and observed when receivers were or were not able to see the snake. Three model snakes made of chicken wire and plaster of Paris were used and painted to resemble either local rhinoceros (*Bitis rhinoceros*) or gaboon vipers (*Bitis gabonica*; fig. S1).

Experiment 2: Simulation of chimpanzee receiver

We exposed the subjects to two sequential stimuli, mimicking scenarios that occur naturally using a within-subjects design (Fig. 2). First, as chimpanzees walked down a path, we played a call from a hidden speaker, simulating the presence of another chimpanzee. After reacting to the playback, the subjects continued to walk down the trial for a further 5 to 10 m. The subjects then saw the second stimulus, a previously placed snake model hidden behind a log (fig. S1), some seconds after hearing the playback (Fig. 2). Using a within-subjects design, we aimed to expose subjects to two trials counterbalanced for call type so that the subjects were played either a rest hoo or one to three alert hoos. Rest hoos are commonly produced in close-range contact contexts not associated with threats, potentially indicating that the simulated caller was unaware of the snake. Alert hoos are highly associated with the presence of hidden threats, potentially indicating awareness of the snake. We kept the call provider per subject constant across conditions to control for influences related to receiver identity. We controlled for receiver behavior, the playback being the only receiver behavior presented. We filmed the trials

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from when subjects approached the speaker to after they either left or had finished looking at the snake model. We conducted 21 trials on 10 subjects. Because we could not completely control which chimpanzee was the first to see the snake, three individuals were exposed twice to the same condition. Playbacks could be heard on the videos. We entered the number of hoos played and whether subjects were alone as control predictors in statistical models.

Playback experiments were conducted from April 2010 to August 2010 and from June 2011 to July 2011, when subjects were alone (n = 9 trials) or in small subgroups (maximum of two other independent chimpanzees), as they walked past or rested within 5 to 10 m of a concealed speaker (Fig. 2). Considerable care was taken that the animals whose call was being played, the "call provider," would not hear their own calls. To this end, one observer followed the call provider and communicated via handheld radios when they were >200 m away from the subject, well beyond the acoustic range of either call type (<100 m).

Considerable care was also taken that the speaker was hidden in dense vegetation 5 to 10 m away from the trail along which the subject was expected to travel. The speaker was positioned at an angle of 60° to 90° from the subject's expected head orientation when walking along the trail. In all trials, the experimenter continuously filmed the subject using a Panasonic NV-GS 330 DV camera with an MKE 400 external Sennheiser microphone for a minimum of 10 s before the playback until at least 10 s after having seen the snake model. Eighteen different stimuli from six call providers [one adult female and one subadult female (individuals KW and RE), three adult males and one subadult male (individuals NK, KT, SQ, and PS)] were used across the 10 subjects. Experiments were not conducted if the subjects traveled with more than two independent other chimpanzees. The "subject" was defined as the first to see the snake to control for habituation effects toward the snake on calling behavior. The strength of social bonds was calculated using the composite relationship index (*47*), and rank differences used matrices based on standard chimpanzee criteria, submissive pant grunt vocalizations [see the study by Wittig *et al.* (*48*) and the Supplementary Materials in that article for analyses]. To avoid habituation to any of the playback stimuli, we conducted experiments below the frequency of naturally occurring hoos, and subjects rarely, if ever, heard playback stimuli on consecutive days (see the Supplementary Materials for further details including variable measured and selection of playback stimuli).

Predictions specific to experiment 2

The sedentary nature of gaboon and rhinoceros vipers (*22*) means that snake models only represent an urgent threat to chimpanzees when in close proximity (<2 m)—the case for all subjects in this experiment but for none of the simulated receivers. A previous primate alarm call playback experiment (*15*) showed that Diana monkeys (*Cercopithecus diana*) who had not previously heard stimuli associated to a specific predator, either an eagle or leopard, called more rapidly upon first presentation of the eagle or leopard call compared to Diana monkeys who had already heard the specific predator-associated vocalization, whether this was a conspecific alarm call or from the predator itself. Taking this into account, if signaling is principally arousal-driven, relating to the signalers' own perspective (H2, signaler habituation hypothesis), then signalers without previous exposure to snake-related stimuli should be more aroused upon finding the snake, and hence, signalers should call more rapidly when naïve to the snake's presence (after hearing a rest hoo rather than an alert hoo).

Crucially, however, if subjects take the receivers' perspective or knowledge into account, then seeing the snake should change the subjects' behavior toward the receivers. The subjects saw the snake model some seconds after hearing the playback of a hoo, but no further receiver behavior was presented. The question is whether the subjects' track the associated shift in the putative receivers' perspective that is provided by the presence of the snake. If the subjects take the receiver's perspective into account, we expected the subjects' attention to the speaker and calling behavior to change after seeing the snake, depending on the call type heard some seconds earlier. A previous study (*28*) showed that a playback of an alert hoo elicited more attention (scans) to the speaker than a rest hoo, where scans are the number of moves of a chimpanzee's head position while looking at the speaker (see the Supplementary Materials). Here, we expected a similar result until the subjects see the snake model. However, after seeing the snake, we expected a shift in speaker-directed attention. For H1 (receiver knowledge), we expected a decline in speaker-directed attention in the alert hoo condition (if the signaler understands the receiver is aware of the snake) but an increase in the rest hoo condition (if the signaler understands that the receiver is not aware of the snake). For H2 (signaler habituation), no such snake-dependent or condition-dependent shift in speaker-directed attention was expected. Instead, the duration in attention given to the snake should be longer in the rest hoo condition (the signaler has no previous information about the snake) than in the alert hoo condition (the signaler has already been primed to the snake's presence).

Thus, H1 and H2 have opposite or different predictions in the following three behavioral variables: calling, marking, and attention given to the snake and the speaker (table S3). Using a playback to simulate a receiver enabled us to keep receiver identity (H3) constant across conditions and to exclude all concurrent behavior reading by receivers, beyond the playback stimulus (H4). We also expected that the subjects' marking and calling might be motivated by present, rather than playback, individuals, in trials where subjects were not alone. To account for this, we coded marking only when marking included gaze alternation between the speaker and the snake. Gaze alternation between other chimpanzees and the snake was not coded as marking. All alert hoos were counted as speaker-directed, because vocalizations are nondiscriminatory for audiences within earshot.

Statistical analysis for experiments 1 and 2

We conducted a series of linear and GLMMs (*49*) using R version 3.0.2 (R Core Team, 2013) and the function lmer for Gaussian, and glmer for binomial and Poisson, models from the package lme4 (*50*). We compared the fit of both full models with that of a respective null model lacking only the test predictors but otherwise being the same as respective full model in all other terms, using a likelihood ratio test. For experiment 1, to test the duration of marking relative to when receivers saw the snake, we ran the GLMM Gaussian model (Fig. 3A). The response variable duration was transformed to log + 1 to comply with model assumptions. Random factors were subject identity, snake placement event, and subject trial per event. Random factors were subject identity and snake placement event (see the Supplementary Materials for further details). No test was conducted for Fig. 3B because the result provided no variation for the test predictor (receiver sees the snake), and the small sample was small.

In experiment 2, to test the impact of the experimental conditions on the subjects' signaling and monitoring behavior, we ran a number of GLMMs to determine the impact of test and control predictors on different signaling behaviors of subjects. In these models, we did not

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include control variables of social bond and dominance rank, because we controlled for social bond by using call providers with a neutral relationship to subjects and because rank did not show significant effects on signaling behavior in experiment 1 (see the Supplementary Materials) (*9*). To correct for multiple testing across GLMMs, we used the permutation-based modification of Fisher's omnibus test to account for nonindependent data (*30*). Gaussian models used maximum likelihood estimates. Binomial models used a logit link function. For all models, we compared the fit of the full model with that of the respective null model lacking only the test predictors but otherwise have the same terms as the respective full model (*51*), using a likelihood ratio test. "Blind"-coded interrater reliability tests on key variables showed good overall interrater reliability: Cohen's $\kappa = 0.74$, $z = 3.7$, $P = 0.002$ (see the Supplementary Materials).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/11/e1701742/DC1

video S1. Western chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Ivory Coast, see real, highly camouflaged rhinoceros viper (www.youtube.com/watch?v=AVXU9C-Oq2k; see fig. S3 for stills).

video S2. Experiment 1 with marking: Kato alert hoos and marks a gaboon viper model for an ignorant receiver with whom he shares a bond (*Pan troglodytes schweinfurthii*, Budongo Forest, Uganda).

video S3. Experiment 1 without marking: Squibbs alert hoos but does not mark a gaboon viper model for ignorant receivers with whom he does not share a bond (*P. troglodytes schweinfurthii*, Budongo Forest, Uganda).

video S4. Experiment 2: Rest hoo condition (*P. troglodytes schweinfurthii*, Budongo Forest, Uganda).

video S5. Experiment 2: Alert hoo condition (*P. troglodytes schweinfurthii*, Budongo Forest, Uganda).

Supplementary Methods

table S1. Source data for experiment 1: Marking behavior in relation to test and control variables.

table S2. Source data for experiment 2: Vocal and nonvocal behaviors of subjects per trial after seeing a snake model.

table S3. Experiment 2: Predictions for receiver knowledge (H1) and signaler habituation (H2) hypotheses.

table S4. Experiment 2: Control predictors have little influence on chimpanzee calling and marking behavior.

fig. S1. Typical scenario upon viper (*B. rhinoceros*) detection by chimpanzees.

fig. S2. Vipers photographed in the Budongo Forest and replica snake models used in the experiments.

References (*52*–*55*)

REFERENCES AND NOTES

1. W. T. Fitch, The evolution of language: A comparative review. *Biol. Philos.* **20**, 193–203 (2005).
2. T. C. Scott-Phillips, *Nonhuman Primate Communication, Pragmatics, and the Origins of Language* (University of Chicago Press, 2015), vol. 56, pp. 56–80.
3. M. Tomasello, Why don't apes point? in *Roots of Human Sociality: Culture, Cognition and Interaction*, N. J. Enfield, S. C. Levinson, Eds. (Oxford, 2006), pp. 506–524.
4. J. Dessalles, Altruism, status, and the origin of relevance, in *Approaches to the Evolution of Language*, J. R. Hurford, M. S. Tuddert-Kenedy, C. Knight, Eds. (Cambridge Univ. Press, 1998), pp. 130–147.
5. C. Heyes, Animal mindreading: What's the problem? *Psychon. Bull. Rev.* **22**, 313–327 (2015).
6. W. T. Fitch, L. Huber, T. Bugnyar, Social cognition and the evolution of language: Constructing cognitive phylogenies. *Neuron* **65**, 795–814 (2010).
7. S. Papworth, A.-S. Böse, J. Barker, A. M. Schel, K. Zuberbühler, Male blue monkeys alarm call in response to danger experienced by others. *Biol. Lett.* **4**, 472–475 (2008).
8. S. A. Wich, H. de Vries, Male monkeys remember which group members have given alarm calls. *Proc. Biol. Sci.* **273**, 735–740 (2006).
9. C. Crockford, R. M. Wittig, R. Mundry, K. Zuberbühler, Wild chimpanzees inform ignorant group members of danger. *Curr. Biol.* **22**, 142–146 (2012).
10. A. M. Schel, S. W. Townsend, Z. Machanda, K. Zuberbühler, K. E. Slocombe, Chimpanzee alarm call production meets key criteria for intentionality. *PLOS ONE* **8**, e76674 (2013).
11. A. B. Hostetter, J. L. Russell, H. Freeman, W. D. Hopkins, Now you see me, now you don't: Evidence that chimpanzees understand the role of the eyes in attention. *Anim. Cogn.* **10**, 55–62 (2007).
12. D. A. Leavens, J. L. Russell, W. D. Hopkins, Multimodal communication by captive chimpanzees (*Pan troglodytes*). *Anim. Cogn.* **13**, 33–40 (2009).
13. W. D. Hopkins, J. P. Taglialatela, D. A. Leavens, Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Anim. Behav.* **73**, 281–286 (2007).
14. J. Fischer, Barbary macaques categorize shrill barks into two call types. *Anim. Behav.* **55**, 799–807 (1998).
15. K. Zuberbühler, D. L. Cheney, R. M. Seyfarth, Conceptual semantics in a nonhuman primate. *J. Comp. Psychol.* **113**, 33–42 (1999).
16. R. M. Seyfarth, D. L. Cheney, Animal cognition: Chimpanzee alarm calls depend on what others know. *Curr. Biol.* **22**, R51–R52 (2012).
17. R. M. Seyfarth, D. L. Cheney, P. Marler, Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Anim. Behav.* **28**, 1070–1094 (1980).
18. M. Groves, F. Thompson, Habituation: A dual-process theory. *Psychol. Rev.* **77**, 419–450 (1970).
19. K. Zuberbühler, R. M. Wittig, Field experiments with nonhuman primates: A tutorial, in *Field and Laboratory Methods in Primatology: A Practical Guide*, D. J. Curtis, J. M. Setchell Eds. (Cambridge Univ. Press, 2011), pp. 207–224.
20. B. C. Wheeler, J. Fischer, Functionally referential signals: A promising paradigm whose time has passed. *Evol. Anthropol.* **21**, 195–205 (2012).
21. S. A. Wich, E. H. M. Sterck, Possible audience effect in Thomas langurs (Primates; *Presbytis thomasi*): An experimental study on male loud calls in response to a tiger model. *Am. J. Primatol.* **60**, 155–159 (2003).
22. J. Penner, C. Fruteau, F. Range, M. O. Rödel, Finding a needle in a haystack: New methods of locating and working with Rhinoceros vipers (*Bitis rhinoceros*). *Herpetol. Rev.* **39**, 310–314 (2008).
23. D. C. Dennett, Intentional systems in cognitive ethology: The "Panglossian paradigm" defended. *Behav. Brain Sci.* **6**, 343 (1983).
24. K. Liebal, S. Pika, J. Call, M. Tomasello, To move or not to move: How apes adjust to the attentional state of others. *Interact. Stud.* **5**, 199–219 (2004).
25. H. Lyn, J. L. Russell, D. A. Leavens, K. A. Bard, S. T. Boysen, J. A. Schaeffer, W. D. Hopkins, Apes communicate about absent and displaced objects: Methodology matters. *Anim. Cogn.* **17**, 85–94 (2014).
26. E. Bates, D. Thal, J. S. Janowsky, Early language development and its neural correlates, in *Handbook of Neuropsychology*, I. Rapin, S. Segalowitz, Eds. (Elsevier, 1992), vol. 7, pp. 69–110.
27. D. A. Leavens, W. D. Hopkins, R. K. Thomas, Referential communication by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **118**, 48–57 (2004).
28. C. Crockford, R. M. Wittig, K. Zuberbühler, An intentional vocalization draws others' attention: A playback experiment with wild chimpanzees. *Anim. Cogn.* **18**, 581–591 (2015).
29. A. G. Rosati, B. Hare, Looking past the model species: Diversity in gaze-following skills across primates. *Curr. Opin. Neurobiol.* **19**, 45–51 (2009).
30. D. M. Potter, D. J. Griffiths, Omnibus permutation tests of the overall null hypothesis in datasets with many covariates. *J. Biopharm. Stat.* **16**, 327–341 (2006).
31. J. Fischer, T. Price, Meaning, intention, and inference in primate vocal communication. *Neurosci. Biobehav. Rev.* 10.1016/j.neubiorev.2016.10.014 (2016).
32. D. L. Cheney, R. M. Seyfarth, Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour* **76**, 25–61 (1981).
33. L. Proops, K. McComb, D. Reby, Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proc. Natl. Acad. Sci. U.S.A.* **106**, 947–951 (2009).
34. T. Bugnyar, S. A. Reber, C. Buckner, Ravens attribute visual access to unseen competitors. *Nat. Commun.* **7**, 10506 (2016).
35. S. J. Shettleworth, Clever animals and killjoy explanations in comparative psychology. *Trends Cogn. Sci.* **14**, 477–481 (2010).
36. S. A. Butterfill, I. A. Apperly, How to construct a minimal theory of mind. *Mind Lang.* **28**, 606–637 (2013).
37. A. Whiten, Humans are not alone in computing how others see the world. *Anim. Behav.* **86**, 213–221 (2013).
38. C. Krupenye, F. Kano, S. Hirata, J. Call, M. Tomasello, Great apes anticipate that other individuals will act according to false beliefs. *Science* **354**, 110–114 (2016).
39. B. Hare, J. Call, M. Tomasello, Do chimpanzees know what conspecifics know? *Anim. Behav.* **61**, 139–151 (2001).
40. J. Kaminski, J. Call, M. Tomasello, Chimpanzees know what others know, but not what they believe. *Cognition* **109**, 224–234 (2008).
41. F. Zimmermann, F. Zemke, J. Call, J. C. Gómez, Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Anim. Cogn.* **12**, 347–358 (2009).

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42. M. Bohn, J. Call, M. Tomasello, The role of past interactions in great apes' communication about absent entities. *J. Comp. Psychol.* **130**, 351–357 (2016).
43. R. A. Gardner, B. T. Gardner, Teaching sign language to a chimpanzee. *Science* **165**, 664–672 (1969).
44. D. Sperber, D. Wilson, Précis of *Relevance: Communication and cognition*. *Behav. Brain Sci.* **10**, 697–754 (1987).
45. K. E. Langergraber, K. Prüfer, C. Rowney, C. Boesch, C. Crockford, K. Fawcett, E. Inoue, M. Inoue-Muruyama, J. C. Mitani, M. N. Muller, M. M. Robbins, G. Schubert, T. S. Stoinski, B. Viola, D. Watts, R. M. Wittig, R. W. Wrangham, K. Zuberbühler, S. Pääbo, L. Vigilant, Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 15716–15721 (2012).
46. N. E. Newton-Fisher, V. Reynolds, A. J. Plumptre, Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest Reserve, Uganda. *Int. J. Primatol.* **21**, 613–628 (2000).
47. C. Crockford, R. M. Wittig, K. Langergraber, T. E. Ziegler, K. Zuberbühler, T. Deschner, Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B* **280**, 20122765 (2013).
48. R. M. Wittig, C. Crockford, T. Deschner, K. E. Langergraber, T. E. Ziegler, K. Zuberbühler, Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B* **281**, 20133096 (2014).
49. R. H. Baayen, *Analyzing Linguistic Data: A Practical Introduction to Statistics Using R* (Cambridge Univ. Press, 2008).
50. D. Bates, M. Maechler, B. Bolker, S. Walker, lme4: Linear mixed-effects models using Eigen and S4 (R package version 1.0-5, 2014).
51. H. Schielzeth, W. Forstmeier, Conclusions beyond support: Overconfident estimates in mixed models. *Behav. Ecol.* **20**, 416–420 (2009).
52. P. Boersma, D. Weenink, Praat: Doing phonetics by computer (version 5.1. 05, 2009).
53. D. J. Barr, R. Levy, C. Scheepers, H. J. Tily, Random effects structure for confirmatory hypothesis testing: Keep it maximal. *J. Mem. Lang.* **68**, 255–278 (2013).
54. A. Field, *Discovering Statistics using SPSS* (Sage Publications, 2005).
55. J. Fox, S. Weisberg, *Car: Companion to Applied Regression*; http://CRAN.R-project.Org/packagecar [accessed 2011].

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