

Wild Chimpanzees Inform Ignorant Group Members of Danger

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Summary

The ability to recognize other individuals' mental states—their knowledge and beliefs, for example—is a fundamental part of human cognition and may be unique to our species. Tests of a “theory of mind” in animals have yielded conflicting results [1–3]. Some nonhuman primates can read others' intentions and know what others see, but they may not understand that, in others, perception can lead to knowledge [1–3]. Using an alarm-call-based field experiment, we show that chimpanzees were more likely to alarm call in response to a snake in the presence of unaware group members than in the presence of aware group members, suggesting that they recognize knowledge and ignorance in others. We monitored the behavior of 33 individuals to a model viper placed on their projected travel path. Alarm calls were significantly more common if the caller was with group members who had either not seen the snake or had not been present when alarm calls were emitted. Other factors, such as own arousal, perceived risk, or risk to receivers, did not significantly explain the likelihood of calling, although they did affect the call rates. Our results suggest that chimpanzees monitor the information available to other chimpanzees and control vocal production to selectively inform them.

Results and Discussion

Recent experiments have demonstrated that animals can understand some of the perceptual or motivational states of others, specifically what they see or intend to do (chimpanzees [4, 5]; monkeys [6, 7]; ravens [8]). What has remained unclear so far is whether the ability to understand and act on others' field of vision or their intentions is the result of reading their behavior or of attributing knowledge, a cognitively more complex process [1–3, 9]. Previous investigations have typically been based on food paradigms, whereby another's ability to see food was equated with its intention to acquire it, which has made it difficult to disentangle intention and perception from knowledge [9]. Alarm-calling behavior provides a useful alternative way of investigating the ability of primates to attribute knowledge. A seemingly costly and altruistic behavior, callers should take into account whether their alarm calls are likely to benefit someone else. There are good theoretical reasons for why individuals should alert other group members

to the presence of danger [10, 11], but little is known about the underlying cognition of such behavior. So far, the only well-established fact is that alarm-call production is influenced by audience composition. For instance, many species produce alarm calls only in the presence of a conspecific (chickens [12]; social mongooses [13]; primates [14]), whereas some require the presence of a particular audience (kin versus non-kin [15, 16]). In primates, there is evidence that individuals also assess the behavior or risk experienced by others during alarm-call production [17, 18]. However, whether alarm calling is further influenced by others' knowledge is currently unknown. For example, baboon mothers do not reply to their offspring's lost call (to facilitate reunification), which has been interpreted as an inability to attribute mental states [19].

When confronted with danger, wild chimpanzees produce two basic types of vocal responses: loud alarm barks and “SOS” screams (typically given after identifying a deadly ambush threat, such as a leopard, python, or neighboring chimpanzee community [20, 21]) or quiet “alert hoo” (typically given to less serious threats but with an ambush-like component, such as snares, highly poisonous vipers, or fresh feces from neighboring chimpanzees or leopards [20]; see [Supplemental Experimental Procedures 1](#) available online). Unlike with the loud alarm calls, snakes have not been observed to move away during quiet alert hoo production. Indeed, it is unlikely that signalers derive immediate benefits from emitting these calls. Rather, alert hoo are acoustically distinct calls that consistently elicit cryptic behavior in receivers, such as silent, cautious approach or silent avoidance behavior (C.C., R.M.W., and K.Z., unpublished data). Vipers are highly camouflaged and can remain static for weeks ([Supplemental Experimental Procedures 2](#)). They have been observed to prey on smaller primates and, if trodden on, can respond with a deadly bite [22]. Thus, although these snakes are not predators of chimpanzees, they are nevertheless highly dangerous to them. Providing information about the presence and specific location of a viper will thus be valuable to others. At the same time, vocal production is costly and may be inhibited if it attracts the attention of predators or hostile individuals from the same or a neighboring group [20, 23]. Taken together, we suggest that costs of calling in situations with a potential ambush threat may be offset by producing a low-amplitude signal when it most benefits receivers, specifically when receivers are unaware of the threat.

Alert hoo production in response to vipers thus offers a possibility to test whether chimpanzee alert hoo production is influenced by receivers' knowledge. To this end, we designed a field experiment in which a subject encountered a motionless but potentially harmful viper model in the presence of others. We made two predictions in relation to our main hypothesis, that is, that alert hoo production is moderated by how much it benefits the receivers. First, if receivers' knowledge state influences alert hoo production, we expected subjects to call less when all receivers were aware of the snake compared to when at least one receiver was still naive. A second prediction was in relation to the callers' own previous experience with the snake model. Under field conditions, it was impossible to systematically control for

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subjects' experience with the snake. Hence, alarm-call production could have been a mere effect of prior exposure, or habituation, to the snake [24, 25]. Here, we predicted that the subjects' calling behavior was influenced by receivers' knowledge state, irrespective of their own previous experience with the snake.

Chimpanzees Take Receiver Knowledge into Account

We observed the responses of members of the Sonso community of Budongo Forest, Uganda, to a snake model positioned on their projected path of travel (Figures S1 and S2). $n = 33$ different individuals saw one of three snake models (males: $n = 8$ adults, $n = 7$ subadults, $n = 1$ juvenile; females: $n = 8$ adults, $n = 8$ subadults, $n = 1$ juvenile; individuals < 6 years old were excluded from analysis). Chimpanzees typically forage in small "parties," i.e., subgroups with regularly changing compositions such that some individuals may not see others for hours or days. Because it was not possible to control the composition of these parties, individuals could serve both as subjects and receivers across the different trials.

We presented snake models 22 times, with each presentation lasting several hours, which resulted in $n = 111$ encounters. Individuals saw a snake model 1–6 times (mean = 2.8). Twenty-two of thirty-three chimpanzees produced alert hoos in response to seeing a model in 46 of 111 encounters (41.4%) and produced "alarm barks" in 3 of 111 encounters (2.7%). In contrast, only 1 of 21 chimpanzees (1 of 42 or 2.4% of encounters) produced alert hoos without seeing the snake but after hearing another group member produce alert hoos in response to the snake. Finally, chimpanzees that had previously seen the snake but could no longer see it alarm called in 3 of 18 encounters (16.7%). Motivation to produce alert hoos may thus be stimulated by seeing the snake (Supplemental Experimental Procedures 9).

Hence, for each trial, any individual who was able to see the snake was termed a "subject," whereas all other individuals present within 50 m of the snake model were termed "receivers." Typically, a party of chimpanzees encountered the snake model as they climbed in or out of a food tree or traveled along a path. The first chimpanzee to see the snake was called the "detector." In these cases, subjects and receivers had no prior exposure to the snake model on that day (31 of 111 cases). In the remaining 80 of 111 cases, subjects saw the snake after another chimpanzee had already detected the snake. In these cases, subjects and receivers usually had some prior exposure to the snake model, having already seen the snake or heard alert hoos. This typically occurred when chimpanzees followed behind a detector, climbed back down a large food tree after feeding, or traveled back along the same path later in the day.

From the moment the first alert hoo was produced, all individuals within earshot (50 m) were considered "knowledgeable" (46 of 111 cases). Individuals who arrived more than 3 min later and were not part of the initial party when the alert hoo was produced were considered "ignorant" (5 of 111 cases). Interestingly, subjects resumed calling as new group members came into view in 3 of 5 cases, independent of the latency since the last call produced (range 5–45 min). Those considered to have "heard" an alert hoo retained their knowledgeable status for the remainder of the day. Thus, receivers were still considered knowledgeable if they were present when the last alert hoo was produced hours earlier (17.7 ± 32.4 min, mean \pm SD), even if they themselves had not seen the snake.

Subject Information and Receiver Information

From the subject's perspective, others' knowledge about the snake fell into three categories: (1) ignorant receivers (no exposure to the snake), (2) partially knowledgeable receivers (heard alert hoos but had not seen the location of snake), or (3) fully knowledgeable receivers (had seen the location of snake; Table S1 and Supplemental Experimental Procedures 4).

As mentioned before, the subjects themselves could have (1) no prior knowledge of the snake (detectors; 31 of 111 cases) or (2) prior knowledge of the snake (heard alert hoos or had seen snake; 80 of 111 cases). Because prior experience might have influenced calling behavior (for example, as a result of habituation [24, 25]), we included this variable in the analysis. Possible confounding variables that might influence subjects' calling behavior were (a–c) level of threat to subject, (d–f) audience composition, (g–i) level of threat to receivers, (j) prior exposure to alert hoos, and (k and l) prior exposure to snake (Table S1).

To test the relative explanatory power of the key predictor variables, Receiver Information and Subject Information, and possible confound variables (a)–(j) on subjects' alarm-calling behavior, we ran two sets of generalized linear mixed models (GLMMs). In each set of models, we tested predictor variables against one of two response variables (Call or Not Call and Number of Calls). Colinearity between predictor variables within each model was low (maximum variance inflation factor = 2.57), apart from Subject Information and Receiver Information (i.e., whether or not subjects or receivers were already aware of the snake), which were highly correlated (Spearman's $r > 0.60$). Thus, we ran parallel analyses for Subject Information and Receiver Information.

Initially, we ran the full sample size (111 cases) for each response variable with predictor variables Subject Information or Receiver Information and possible confound variables (a)–(h) and (j). However, because Receiver Approach (variable i) had values for only 100 of 111 encounters, we ran a reduced data set of 100 cases for both response variables, which allowed us to include the predictor variable Receiver Approach (Table S2).

We found that the key variables, Receiver Information and Subject Information (whether receivers and subjects were already aware of the snake, either by having seen it or by having heard alert hoos), were the only predictors showing significance or a trend in all models (Figure 1; Tables 1 and S1; Supplemental Experimental Procedures 5).

Additional predictor variables were significant in different models (Supplemental Experimental Procedures 7). In models with response variable Call or Not Call, the only other significant predictor was Subject Closer Than Receivers. In models with response variable Number of Calls, two other variables were consistently significant: Strong Bond Partner Present and Subject Startled (Tables 1 and S2). Equally relevant, the predictors Subject Total Model Encounters, Subject Distance to Snake, Receiver Distance to Snake, Number of Receivers, and Number of Dominant Receivers did not contribute significantly to the response variables in any model (Tables 1 and S2), indicating that any influence they may have on calling behavior is less pronounced than that of the significant variables in these models (Supplemental Experimental Procedures 7).

Prior Snake Experience as a Possible Confound

Because Receiver Information and Subject Information were confounded, we ran a third set of models to distinguish which



Figure 1. Influence of Receiver Information on Subjects' Likelihood to Emit Alert Hoos upon Seeing the Snake Model

Black indicates no alarm calls produced; gray indicates at least one alarm call produced. "Receiver information" indicates receiver ignorance or knowledge from the perspective of the subject, divided into the following three categories. "Seen" indicates knowledgeable receivers: the subject had seen all receivers see the snake model. "Heard" indicates partially knowledgeable receivers: the subject had heard an alarm call when all receivers were within 50 m of the snake model but could not have seen all receivers see the snake model. "Ignorant" indicates that the subject could not have seen all receivers see the snake and had not heard an alert hoo when all current receivers were within earshot (50 m) of the alert hoo.

of these were driving calling behavior. Specifically, we asked whether subjects' calling behavior was principally influenced by their own previous exposure, or habituation, to the snake, as opposed to their awareness of receivers' knowledge about the snake. To control for subjects' differing levels of prior snake exposure, we only included cases where both subjects and receivers were previously aware of the snake model (Supplemental Experimental Procedures 5). In addition, to minimize confounds from other significant variables, we only included cases where receivers were further away from the snake than subjects and receivers were approaching the snake ($n = 15$ subjects, 30 cases).

In these cases, Receiver Information varied, with some receivers having heard alert hoos only (no knowledge of location) and others having seen the snake (knowledge of location). We thus included the predictor variable Receiver Information and two measures of subjects' prior exposure to the snake, Subject Already Called (subjects had or had not previously produced alert hoos) and Duration of Subject Exposure [time since subject was first aware of the snake until the subject saw the snake on this occasion: median (quartiles) 8.0 (1.3, 64.25) min; variables (k) and (l); Table 2].

We ran two models with both response variables and crucially found that only Receiver Information was significant in each model (Table 2), indicating that subjects' calling behavior was primarily influenced by the knowledge state of receivers, and not by subjects' own prior experience with the snake model (Supplemental Experimental Procedures 5 and 6).

Finally, observers' sex and age class influenced neither the likelihood of calling (two-way analysis of variance [ANOVA]: sex: $F_{1,29} = 0.27$, $p = 0.609$; age: $F_{1,29} = 0.06$, $p = 0.811$; interaction: $F_{1,28} = 0.06$, $p = 0.811$) nor the average number of calls produced (two-way ANOVA: sex: $F_{1,29} = 0.003$, $p = 0.96$; age: $F_{1,29} = 0.51$, $p = 0.480$; interaction: $F_{1,28} = 0.67$, $p = 0.419$) (Supplemental Experimental Procedures 7).

Table 1. Effect of Receiver Information and Other Predictor Variables on Chimpanzee Alert Hoo Production upon Seeing a Snake Model

Predictor Variables	Estimate	SE	z	p
Response Variable: Call or Not Call				
Intercept	-0.33	1.50	-0.22	0.825
Receiver Information	-0.96	0.44	-2.17	0.030**
Subject Total Model Encounters	-0.73	0.45	-1.64	0.101
Subject Startled	0.11	0.80	0.14	0.886
Subject Distance to Snake	-0.22	0.36	-0.62	0.534
Latency since Last Call	0.70	0.73	0.95	0.341
Strong Bond Partner Present	0.71	0.55	1.29	0.198
Number of Receivers	-0.22	0.46	-0.48	0.631
Number of Dominant Receivers	0.19	0.40	0.46	0.644
Receiver Distance to Snake	0.08	0.34	0.25	0.804
Subject Closer Than Receivers	1.15	0.61	1.87	0.062*

Response Variable: Number of Calls				
Intercept	0.83	0.52	1.61	0.107
Receiver Information	-0.50	0.14	-3.63	0.000**
Subject Total Model Encounters	-0.07	0.14	-0.50	0.618
Subject Startled	0.48	0.20	2.38	0.017**
Subject Distance to Snake	-0.09	0.11	-0.82	0.412
Latency since Last Call	-0.28	0.24	-1.17	0.242
Strong Bond Partner Present	0.72	0.16	4.38	0.000**
Number of Receivers	0.00	0.08	0.02	0.99
Number of Dominant Receivers	0.09	0.17	0.55	0.581
Receiver Distance to Snake	-0.01	0.10	-0.11	0.911
Subject Closer Than Receivers	0.32	0.21	1.56	0.118

Receiver Information indicates receivers' prior exposure to snake-related stimuli, from the perspective of the subject. Models were run with different response variables: Call or Not Call (top) and Number of Calls (bottom). Both models included all 111 cases and predictor variables (a)-(h) and (j). Both models were repeated with Subject Information replacing highly correlated Receiver Information and obtaining very similar results. * $p < 0.1$; ** $p < 0.05$. See Table S1 for predictor variable definitions and predictions. As a result of the rarity of snake model presentation opportunities, our criteria for independence of data points were as follows: (1) a chimpanzee who sights the snake model becomes a subject or (2) a new receiver arrives within 50 m of the snake model. A maximum of two simultaneous subjects were included as data points (the two closest to the snake) until either could no longer see the snake. This led to $n = 111$ subject "encounters" from 33 chimpanzees during 22 snake model presentations (mean \pm SD: duration of snake presentations, 110.5 ± 60.4 min; duration of subject encounters, 5.25 ± 8.4 min; number of receivers across 111 encounters, 7.2 ± 5.2). To control for pseudoreplication, three random factors were included in each model: Subject's Identity, Snake Model used (model 1, 2, or 3) and Model Presentation Event (with each event lasting up to one day) (Supplemental Experimental Procedures 7).

Factors Influencing the Likelihood of Alarm Calling

Upon seeing the snake model, the likelihood of alarm calling (Call or Not Call) did not depend on subjects' own perceived risk or level of habituation, receiver composition, or receivers' level of risk (Supplemental Experimental Procedures 6). Significant effects were found for Receiver Information (and a trend for Subject Closer Than Receivers). Model estimates showed that, for Receiver Information, subjects were less likely to call with increasing information available to receivers about the specificity of the danger. As shown in our first analysis, subjects called most if receivers had no exposure to the snake. They called less if receivers had heard alert hoos, and they called least if receivers had seen the snake model, suggesting that they took into account how much information receivers had about the type and position of the danger (Table 1; Figure 1). Model estimates for Subject Closer Than Receivers showed that subjects called more when they were closer to the snake than any receiver. This was not correlated to their

Table 2. Influence of Subjects' Prior Exposure and Receivers' Knowledge on Chimpanzee Alert Hoo Production when Seeing the Snake Model

Predictor Variables	Estimate	SE	z	p
Response Variable: Call or Not Call				
Intercept	-0.81	1.31	-0.61	0.539
Receiver Information	-2.97	1.25	-2.37	0.018**
Subject Already Called	1.77	1.20	1.47	0.142
Duration of Subject Exposure	0.20	0.22	0.87	0.384
Response Variable: Number of Calls				
Intercept	1.33	0.37	3.61	0.000
Receiver Information	-1.19	0.29	-4.03	0.000**
Subject Already Called	0.32	0.26	1.24	0.215
Duration of Subject Exposure	0.00	0.06	0.02	0.987

Both models included 30 cases where subject and receivers had prior information about the snake (i.e., they had already heard alert hooes and may or may not have seen the snake). Thus, no cases are included in this model when subjects were the first to detect the snake. Likewise, Receiver Information included only "heard" and "seen" cases, and no "ignorant" cases. Different response variables were used for each: Call or Not Call (top) and Number of Calls (bottom). **p < 0.05. Subject Already Called (y/n): subject had or had not already produced alert hooes to the snake model, variable (k); Duration of Subject Exposure (min): time since subject was first aware of snake until subject saw the snake on this occasion (median [quartiles]: 8.0 [1.3, 64.25] min), variable (l). See Table S1 for full variable definitions and predictions.

own or the receivers' absolute distance to the snake and thus suggests that subjects made an assessment of their relative proximity to the snake before calling.

Factors Influencing the Amount of Calling

Compared to the likelihood of calling (Call or Not Call), the response variable Number of Calls was significantly influenced by Subject Startled and when Strong Social Bond Partners were among receivers, in addition to Receiver Information (Tables 1 and S2). Startle responses, which typically occur across animals within <100 ms of a stimulus [26, 27], were temporally dissociated from the production of alert hooes. Alert hooes were emitted 1.70 ± 0.4 s (mean \pm SD) after having seen the snake and 0.91 ± 0.63 s after the end of the startle response, suggesting that alert hooes are not components of the startle response, nor necessarily of heightened arousal as is frequently assumed by some authors (e.g., [28]). The "social bond" effect suggests that, like other species [15], chimpanzees are more motivated to call if they can benefit valuable group members.

In one model, two extra variables were significant, when receivers were approaching the snake (Receiver Approach) and when the Latency since Last Call was relatively long (Table S2). The Receiver Approach effect suggests that subjects perceived others' intentions to pass close by the snake (and their forthcoming exposure to danger). Again, receivers' absolute distance to the snake had no effect, further suggesting that subjects assessed others' intentions and implied risk, regardless of the caller's own prior experience with the snake.

Conclusions and Implications

We have shown that chimpanzee alarm-calling behavior was driven not only by perceived danger but also by whether others were aware of the danger. The likelihood of calling was not related to the subjects' or receivers' perceived risk, was independent of receiver composition, and was not primarily driven by subjects' habituation to snake-related stimuli. Once a chimpanzee began alarm calling, the number of calls produced was

subject to additional influences. Personal risk, risk to a valuable receiver, and risky behavior by a receiver all had enhancing effects, which is in line with other alarm-call studies showing that the strength of the alarm-calling response is influenced by the risk faced by subjects or receivers [14–18].

The fact that alarm-call production was more likely when receivers had less information about the danger has not been documented before. Unlike alarm-call systems in other species, it implies that chimpanzees keep track of information available to receivers and intentionally inform those who lack certain knowledge. It is known that monkeys are adept at keeping track of their own and others' relationships, that they remember details of specific interactions that happened some minutes ago, and that they make inferences about current interactions based on the recent memory of previous ones [1, 6, 29, 30]. Here, our results indicate that chimpanzees keep track of what others can or cannot have seen and heard and communicate missing information that is relevant and beneficial to receivers. These results extend the current literature in four ways. First, they challenge current opinion that it is unlikely that nonhuman animals integrate recognition that others are ignorant with provision of the missing information through communication [31]. Second, our study is in line with recent studies suggesting that chimpanzees have a degree of volitional control over vocal production ([23, 32, 33], but see [28]). Third, there is mixed support suggesting that chimpanzees exhibit prosocial behavior (for, [34, 35]; against, [36]). Here we show that chimpanzee vocal behavior is influenced by a prosocial motivation, namely intentionally informing others of danger. Finally, our results are particularly relevant to debates about the role of mental state attribution in the evolution of language. Some scientists have argued that a crucial stage in this evolution occurred when individuals began producing vocalizations with the goal of informing and thereby reducing ignorance in others [37, 38].

Experimental Procedures

Subjects and Vocal and Behavioral Observations

R.M.W. and C.C. collected data from the habituated Sonso community in the Budongo Forest, Uganda, from February 2008 to July 2010 (www.budongo.org). We manufactured three models of dangerous venomous snakes familiar to the chimpanzees, two gaboon vipers (*Bitis gabonica*) and one rhinoceros viper (*Bitis nasicornis*), using wire mesh, plaster, acrylic paint, and varnish (Figure S2 and Supplemental Experimental Procedures 2). We recorded hoo calls during snake encounters using Marantz PMD660 solid-state recorders and Sennheiser MKH416 and MKH418 directional microphones. Social dominance relationships were determined via pant-grunting vocalizations, a reliable indicator of subordination in chimpanzees [20]. Males and females were assigned as high, mid, or low ranking. We calculated subject's strong social bond partners using relative rates of affiliative and aggressive behaviors in a derivative of the composite sociality index (Supplemental Experimental Procedures 8).

Experimental Design

In pilot trials, we found that models of gaboon and rhinoceros vipers consistently triggered vocal behavior with alert hooes only (Figure S1; Movies S1 and S2). Experiments were conducted between September 2008 and December 2009 and between April and July 2010. During this period, we successfully presented a snake model on 22 different occasions. We kept presentations within the natural rate of encounters in which human observers saw these snake species (natural rate: mean = 1.8 per month, range 0–15; Supplemental Experimental Procedures 2).

Experimental Trials

For each trial, two human observers were within 10 m of the model while two or three others awaited the chimpanzees 50–100 m away on anticipated approach paths. Motorola GP340 radios were used to update human

observers on all relevant movements and changes in party composition. All approaching individuals were video recorded with a Panasonic DV video camera. For each trial, we noted (1) the time of arrival and departure of all individuals within a 50 m and 100 m range (maximum range that subjects could see receivers or only hear alert hoos, respectively), (2) individuals' identity, (3) their absolute and (4) relative distance to the snake model after snake model detection, (5) the time of snake model detection, and (6) the vocal behavior of all individuals within a 50 m radius of the snake (Supplemental Experimental Procedures 3).

Analysis of the Effect of Observer and Receiver Behavior on Alarm Call Production

Video recordings were analyzed with Adobe Premier software and combined with direct observational data and audio recordings (Movies S1 and S2). We ran GLMMs in R (version 2.11.1) using the function lmer provided by the R package lme4 [39] (Supplemental Experimental Procedures 7).

Supplemental Information

Supplemental Information includes two figures, two tables, two movies, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.11.053.

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References

- Cheney, D.L., and Seyfarth, R.M. (2007). Baboon Metaphysics: The Evolution of a Social Mind (Chicago: Chicago University Press).
- Call, J., and Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci. (Regul. Ed.)* 12, 187–192.
- Fitch, W.T., Huber, L., and Bugnyar, T. (2010). Social cognition and the evolution of language: constructing cognitive phylogenies. *Neuron* 65, 795–814.
- Hare, B., Call, J., and Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Anim. Behav.* 61, 139–151.
- Kaminski, J., Call, J., and Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition* 109, 224–234.
- Engh, A.L., Hoffmeier, R.R., Cheney, D.L., and Seyfarth, R.M. (2006). Who, me? Can baboons infer the target of vocalizations? *Anim. Behav.* 71, 381–387.
- Burkart, J., and Heschl, A. (2007). Understanding visual access in common marmosets, *Callithrix jacchus*: Perspective taking or behavior reading? *Anim. Behav.* 73, 457–469.
- Bugnyar, T. (2011). Knower-guesser differentiation in ravens: others' viewpoints matter. *Proc. Biol. Sci.* 278, 634–640.
- Cheney, D.L. (2011). Extent and limits of cooperation in animals. *Proc. Natl. Acad. Sci. USA* 108 (Suppl 2), 10902–10909.
- Smith, S.F. (1978). Alarm calls, their origin and use in *Eutamias sonomae*. *J. Mammal.* 59, 888–893.
- Zuberbühler, K. (2009). Survivor signals: the biology and psychology of animal alarm calling. *Adv. Stud. Behav.* 40, 277–322.
- Karakashian, S.J., Gyger, M., and Marler, P. (1988). Audience effects on alarm calling in chickens (*Gallus gallus*). *J. Comp. Psychol.* 102, 129–135.
- Le Roux, A., Cherry, M.I., and Manser, M.B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Anim. Behav.* 75, 943–949.
- Wich, S.A., and Sterck, E.H.M. (2003). Possible audience effect in Thomas langurs (*Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *Am. J. Primatol.* 60, 155–159.
- Hoogland, J.L. (1983). Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). *Anim. Behav.* 31, 472–479.
- Cheney, D.L., and Seyfarth, R.M. (1985). Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 94, 150–166.
- Papworth, S., Böse, A.S., Barker, J., Schel, A.M., and Zuberbühler, K. (2008). Male blue monkeys alarm call in response to danger experienced by others. *Biol. Lett.* 4, 472–475.
- Wich, S.A., and de Vries, H. (2006). Male monkeys remember which group members have given alarm calls. *Proc. Biol. Sci.* 273, 735–740.
- Rendall, D., Cheney, D.L., and Seyfarth, R.M. (2000). Proximate factors mediating 'contact' calls in adult female baboons and their infants. *J. Comp. Psychol.* 114, 36–46.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior* (Cambridge, MA: Harvard University Press).
- Crockford, C., and Boesch, C. (2003). Context specific calls in wild chimpanzees: analysis of barks. *Anim. Behav.* 66, 115–125.
- Penner, J., Fruteau, C., Range, F., and Rödel, M.-O. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (*Bitis rhinoceros*). *Herpetol. Rev.* 39, 310–314.
- Wilson, M., Hauser, M., and Wrangham, R. (2007). Chimpanzees modify grouping and vocal behaviour in response to location specific risk. *Behaviour* 144, 1621–1653.
- Fischer, J. (1998). Barbary macaques categorize shrill barks into two call types. *Anim. Behav.* 55, 799–807.
- Zuberbühler, K. (1999). Conceptual semantics in a non-human primate. *J. Comp. Psychol.* 113, 33–42.
- Eaton, R.C., Bombardieri, R.A., and Meyer, D.L. (1977). The Mauthner-initiated startle response in teleost fish. *J. Exp. Biol.* 66, 65–81.
- Gillon, C., Ameli, R., Woods, S.W., Merikangas, K., and Davis, M. (1991). Fear-potentiated startle response in humans: effects of anticipatory anxiety on the acoustic blink reflex. *Psychophysiology* 28, 588–595.
- Owren, M.J., and Rendall, D. (2001). Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evol. Anthropol.* 10, 58–71.
- Crockford, C., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2007). Baboons eavesdrop to deduce mating opportunities. *Anim. Behav.* 73, 885–890.
- Wittig, R.M., Crockford, C., Wikberg, E., Seyfarth, R.M., and Cheney, D.L. (2007). Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc. Biol. Sci.* 274, 1109–1115.
- Tomasello, M., Call, J., and Hare, B. (2003). Chimpanzees understand psychological states - the question is which ones and to what extent. *Trends Cogn. Sci. (Regul. Ed.)* 7, 153–156.
- Crockford, C., Herbinger, I., Vigilant, L., and Boesch, C. (2004). Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology* 110, 221–243.
- Slocombe, K.E., and Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proc. Natl. Acad. Sci. USA* 104, 17228–17233.
- Melis, A.P., Warneken, F., Jensen, K., Schneider, A.C., Call, J., and Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proc. Biol. Sci.* 278, 1405–1413.
- Warneken, F., and Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science* 311, 1301–1303.
- Silk, J.B., Brosnan, S.F., Vonk, J., Heinrich, J., Povinelli, D.J., Richardson, A.F., Lambeth, S.P., Mascaró, J., and Schapiro, G. (2005). Chimpanzees are indifferent to the welfare of other group members. *Nature* 435, 1357–1359.
- Pinker, S. (1994). *The Language Instinct* (New York: William Morrow and Sons).
- Seyfarth, R.M., and Cheney, D.L. (2010). Production, usage, and comprehension in animal vocalizations. *Brain Lang.* 115, 92–100.
- Bates, D. and Maechler, M. (2010). lme4: Linear mixed-effects models using Eigen and R syntax. R package version 0.999375-35 (<http://lme4.r-forge.r-project.org/>).