

Kent Academic Repository

Full text document (pdf)

Citation for published version

Wheeler, Brandon C and Fischer, Julia (2015) The blurred boundaries of functional reference: a response to Scarantino & Clay. *Animal Behaviour*, 100 . e9-e13. ISSN 0003-3472.

DOI

<https://doi.org/10.1016/j.anbehav.2014.11.007>

Link to record in KAR

<http://kar.kent.ac.uk/53204/>

Document Version

Publisher pdf

Copyright & reuse

Content in the Kent Academic Repository is made available for research purposes. Unless otherwise stated all content is protected by copyright and in the absence of an open licence (eg Creative Commons), permissions for further reuse of content should be sought from the publisher, author or other copyright holder.

Versions of research

The version in the Kent Academic Repository may differ from the final published version.

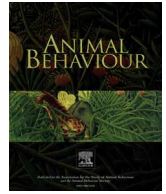
Users are advised to check <http://kar.kent.ac.uk> for the status of the paper. **Users should always cite the published version of record.**

Enquiries

For any further enquiries regarding the licence status of this document, please contact:

researchsupport@kent.ac.uk

If you believe this document infringes copyright then please contact the KAR admin team with the take-down information provided at <http://kar.kent.ac.uk/contact.html>



Forum

The blurred boundaries of functional reference: a response to Scarantino & Clay



Brandon C. Wheeler^{a, b, *}, Julia Fischer^a

^a Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany

^b School of Anthropology & Conservation, University of Kent, Canterbury, U.K.

ARTICLE INFO

Article history:

Received 2 November 2014

Initial acceptance 6 November 2014

Final acceptance 6 November 2014

Available online 6 December 2014

MS. number: AF-14-00879

Keywords:

affect
animal communication
cognition
decision making
functional reference
information
language evolution
meaning

The past years have shown a resurgence of interest in conceptual issues in animal communication, with much of the debate centering on the concept of information (e.g. Carazo & Font, 2010; Rendall, Owren, & Ryan, 2009; Ruxton & Schaefer, 2011; Scarantino, 2010; Scott-Phillips, 2008; Seyfarth et al., 2010), and whether the identification of so-called ‘functional reference’ contributes to a better understanding of linguistic reference, and ultimately the evolution of speech (Fedurek & Slocombe, 2011; Manser, 2013; Townsend & Manser, 2013; Wheeler & Fischer, 2012). Scarantino and Clay’s (2015; hereafter S&C) Forum article in this issue continues this debate, and is largely a response to a recent paper of ours (Wheeler & Fischer, 2012). In our original paper, we contended that all cases of animal communication in which receiver responses could be explained in terms of the information provided by the signal could be said to function referentially. According to most definitions, this applies to the entire spectrum of animal communication (see Rendall et al., 2009). Because the boundaries of ‘functional reference’ have been blurred to a degree where it is no

longer productive to distinguish between functionally referential communication and communication more generally, we suggested to abandon the term altogether. In addition, we argued that the original motivation to study ‘referential’, ‘semantic’ or ‘symbolic’ communication in animals was to search for the substrate that gave rise to referential communication in human speech. Once it became clear that functionally referentially calls most likely do not share central criteria for linguistic reference, and therefore do little to illuminate the origins of linguistic reference, the concept lost much of its allure, at least to us. We further suggested an alternative framework that aims to elucidate the potential cognitive mechanisms underpinning receiver behaviour. Specifically, we suggested to distinguish between ‘meaning attribution’ and ‘decision making’, and to consider the role of additional sources of information, such as contextual variation on both.

In their article, S&C take another route, and argue that it would be more productive to retain the term ‘functional reference’ but redefine what would constitute such a signal. Moreover, they criticize our notion of meaning attribution in animals. We find much to both agree and disagree with in S&C’s proposal. Considering their paper as a whole, most of the disagreement between their perspective and our own seems to be a rather simple difference in preferred terminology rather than a fundamental difference

* Correspondence: B. C. Wheeler, School of Anthropology & Conservation, University of Kent, Canterbury, Kent CT2 7NR, U.K.

E-mail address: bcwheeler43@gmail.com (B. C. Wheeler).

regarding the nature of animal communication. Indeed, a substantial part of their paper is an attempt to formalize the roles of information and context and their relevance for signal receivers, and we find these contributions to be both insightful and largely consistent with the alternative framework we propose. At the same time, we disagree with S&C on a number of points and believe that it ultimately underscores the strengths of our proposed framework for conceptualizing the cognitive mechanisms involved in signal perception.

SENDERS VERSUS RECEIVERS AND THE LEVELS OF ANALYSIS

The concept of functional reference was introduced to acknowledge that some signals appeared to function in the same way as human words while the proximate mechanisms that underpinned the production of such signals essentially remained unclear (Marler, Evans, & Hauser, 1992). Yet, despite professed neutrality regarding the cognitive mechanisms underpinning functionally referential communication, a distinction was made from the beginning between referential and emotional aspects of animal signalling; that is, at the level of the mechanisms (Marler et al., 1992). Although, initially, emotional and symbolic aspects of animal communication were pitted against each other (Marler, 1984), it was later conceded that these two aspects were not mutually exclusive, insofar as a given signal could simultaneously have both referential and emotional components, just as a human speaker's current emotional state will have some effect on the structure of a given linguistic utterance, but emotion and reference were nevertheless considered distinct aspects at the mechanistic level (Marler et al., 1992). A purely emotional signal would thus not qualify as referential, indicating that the mechanistic-agnosticism of functional reference had its limits.

It was more than a decade later that Seyfarth and Cheney (2003) pointed out that the mechanisms underpinning signal production in most animals are unrelated to the mechanisms that are involved in the perception of those same signals. The distinction between emotion and reference was, they claimed, like comparing apples and oranges, not because a given signal could potentially have both emotional and referential components as Marler et al. (1992) correctly pointed out, but because emotion is best seen as related to signal production, while the referential aspects applied to the receiver. That is, a signal could be purely emotional in its production, but, if the signal's production shares a predictable relationship with the occurrence of something salient to receivers, then the potential exists for receivers to take the signal as being indicative of that salient phenomenon. Wheeler and Fischer's (2012) argument was largely based on this insight: the production of most signals, even in species with relatively well-developed cognitive abilities, appears indeed to be based on very different mechanisms than those involved in the production of language, but there may be some degree of cognitive continuity in the mechanisms involved in the comprehension of calls and language on the side of the receivers (but see Scott-Phillips, *in press*). At least in some cases, recipients learn through experience that a given signal is associated with a given phenomenon, and this learning explains their responses to one degree or another (but see Owren & Rendall, 2001; Rendall et al., 2009 for extended discussions of factors affecting lower-level responses).

Although S&C do not make an explicit distinction between senders and receivers, they do so implicitly by setting no limits on what mechanisms should underpin the production of functionally referential signals, while limiting such designation to cases in which receivers 'take the call to stand for' something (and thus excluding cases in which behavioural responses are driven solely by, for example, neuroendocrine processes). S&C thus seem truly

agnostic regarding the mechanisms underlying signal production, leading them to advocate for the extension of the realm of possible 'referents' to include phenomena that are considered 'internal' to the signaller. Such a conception of 'referent' is in line with that suggested by Smith (1981); it contrasts, though, with that of the originators of the concept of functional reference (Macedonia & Evans, 1993; Marler et al., 1992), and it is this change that arguably does more to move functional reference away from its original conception than do the proposed changes to the production and perception criteria that S&C largely focus on.

The suggestions to remove the distinction between internal and external 'referents' and to eliminate the focus on context specificity in both signal production and signal perception are fully in concordance with our own suggestions (Wheeler & Fischer, 2012). Indeed, despite some disagreements about the weight given to different lines of evidence, it seems that when S&C would conclude that 'signal *x* functionally refers to *y*', we would likewise tend to conclude that 'the receiver has attributed the meaning *y* to the signal', and vice versa. That the difference is largely terminological is evinced by the fact that S&C equate their conception of functional reference with receivers taking a signal *x* to 'stand for' a phenomenon *y*; it is hard to see this as much more than a slightly different way of saying that the receiver attributes the meaning *y* to the signal. The differences between our perspectives regarding what evidence might be necessary for one to draw the conclusion that *x* means (or 'refers to', or 'stands for') *y* for a given receiver may be a point of genuine disagreement, but this is a separate issue from which set of terminology (or even which conceptual framework) one prefers; one could easily adopt their criteria and our terminology or vice versa, and one should not conflate these realms as S&C appear to do.

Our rejection of the term 'functional reference' and embracement of 'meaning attribution' stems from an explicit consideration of the distinction between signallers and receivers. While referring to something (in the original sense) is a behaviour performed by the sender, attributing meaning to a signal is something done by a receiver. What we know about the proximate mechanisms involved in most forms of animal communication (including but not limited to vocal communication in most mammals) preclude the signals from being referential in the way that words in human language are (Wheeler & Fischer, 2012). At the same time, the behavioural responses of receivers are shaped by experience in a way that suggests that receivers are indeed attributing what can legitimately be called 'meaning' to signals. We suggested that this is possible not because the signals carry symbolic meaning, but because they carry a type of 'natural meaning' (*sensu* Grice, 1957), which is instantiated when natural spatiotemporal associations between two phenomena lead to the occurrence of one entailing the occurrence of the other; this is not unlike the production of a signal correlating with the occurrence of another event (Scarantino, 2010; Scott-Phillips, *in press*; Wharton, 2003). In contrast, the idea that signallers are referring to things appears to be, at best, an analogy. In other words, because animal signals have natural meaning, we are perhaps able to empirically address the question 'what does that signal mean to a monkey?' In contrast, when animal signals lack symbolic meaning, the questions 'what did that monkey mean by producing that signal?' or 'what was that monkey referring to?' are ill-posed (see Grice, 1957).

S&C are correct that our application of the term 'natural meaning' to animal signals in many cases falls outside the boundaries of Grice's (1957) concept (S&C's criticism that we can do playbacks of snake alarms in the absence of snakes is not a good argument, though, as experimental manipulations could be applied to any of Grice's actual examples to argue that natural meaning does not exist at all; but we concede that the fact that naturally

occurring snake alarms can occur in the absence of snakes is a fair criticism). The problem stems from the fact that Grice's dichotomy of natural and non-natural meaning is not exhaustive, even as applied as intended to human communication, but applying the concept to encompass animal signalling requires only relatively minor modifications to Grice's conception of natural meaning (Wharton, 2003). Importantly, the difference between strict Gricean natural meaning and the correlational meaning of animal signals is one of degree, whereas the difference between this type of meaning and the non-natural (symbolic) meaning that is based on social conventions and characterises language is one of kind (Deacon, 1997; Fitch, 2010; Scott-Phillips, *in press*; Wharton, 2003; Wheeler & Fischer, 2012).

Strictly speaking, most animal signals probably do have Gricean natural meaning, with that meaning being the internal state or states associated with the production of the signal. But the meaning that a receiver attributes to a given signal (or, in other words, what the receiver takes the signal to indicate about its world) is in only rare cases going to be this internal state of the receiver. Rather, we contend that, at least in species without the ability to understand that others have internal states, the receiver's attributed meaning must be some phenomenon it is capable of directly observing and that is to some extent reliably associated with the signal's production. This phenomenon can be something completely external to the signaller, such as a predator, food or conspecific competitor, or what is typically considered more internal to the signaller, such as its subsequent behaviour or fighting ability. In other cases, receivers respond adaptively to a signal even when its relevant correlate (e.g. probability of conception) is unlikely to be observable (e.g. male baboons varying their mating effort based on the size of the swelling of a female's anogenital region; Zinner, Nunn, van Schaik, & Kappeler, 2004); in these cases, it would not seem to make sense to interpret the responses in terms of meaning attribution, but instead as an innate response to the signal.

Thus the strict Gricean natural meaning of a signal will in most cases differ from the meaning that a receiver attributes to the signal, although the two are clearly related concepts because they are both based on the natural spatiotemporal associations that exist between the signal and its meaning. Furthermore, there is precedent and growing momentum to explicitly apply Grice's concepts, and at least the 'natural' portion of his terminology, to describe the nature of meaning in animal signals ('natural information': Scarantino, 2010; 'natural code': Wharton, 2003; Scott-Phillips, *in press*).

In summary, many animals appear to make learned associations between receiving a given signal and the occurrence of some other relevant phenomenon. Once that learned association is in place, then receivers are in a position to make predictions regarding what is likely to occur following the perception of the signal. In such cases it seems fair to say that the receiver takes the signal to mean *y* (or, perhaps to speak less ambiguously, that it indicates *y*). The fact that receivers respond adaptively *as if* responding to that phenomenon itself may be necessary but it is certainly not sufficient to conclude that the responses are driven proximately by meaning attribution, as this is only one possible mechanism that may underlie such adaptive responses. Diagnosing meaning attribution thus requires one to take a broad perspective to infer, if not directly investigate, the proximate mechanisms that underlie receiver responses.

PROBLEMS WITH THE CRITERIA FOR DIAGNOSING 'NEW' FUNCTIONAL REFERENCE

Much of S&C's argument that sticking with functional reference is a better way forward rests on their contention that they have

provided unambiguous diagnostic criteria for future authors to rely on. S&C's key move is to combine a signal and its context to create a 'unit of functional reference' (p. e4). Following Scarantino (2013), functional reference is now operationalized the following way: 'a signal of type X in context C functionally refers to, or means_R, a state of affairs of type Y if (1) Xs in context C correlate with Ys [...] (information criterion), and (2) presentations of Xs in context C and in the absence of Ys reliably elicit contextually adaptive responses in receivers specific to Ys (response criterion).' The fundamental problem here is that *all* signals will now meet the modified production criterion, because all that is required is that a researcher breaks context down into sufficiently small categories that, within each category, the signal has some association with some given phenomenon. As a consequence, it would also be impossible to distinguish between truly referential signals (if they existed) and most other signals.

The only potential cases of animal signalling to not meet S&C's criteria would therefore be those systems in which receiver responses are not adaptive to the receiver (e.g. sensory bias exploitation; Ryan, 1990). However, such cases do not fall under most definitions of communication or signalling, which either explicitly limit communication to cases in which receiver responses are adaptive for the receiver (Maynard Smith & Harper, 2003; Scott-Phillips, 2008), or to cases in which information is conveyed (e.g. Bradbury & Vehrencamp, 2011). It thus seems difficult to come up with an example of a signalling system, falling under these definitions, in which the perception criteria would not be likely to be met. While S&C require that the responses be adaptive even in the absence of the referent, cases in which the supposed referent is not observable to the receiver (e.g. the referent is internal to the signaller and is never observable, or is only observable some time after the signal is produced, as in the case of the signaller's subsequent behaviour) provide a sort of natural experiment which suggests that such adaptive responses occur widely in the absence of an observable referent.

S&C go on to argue that they would not in fact consider all signals to be functionally referential, but in order to do so they are forced to go beyond their supposedly 'diagnostic' criteria. For example, even if both criteria are met, S&C do not consider all adaptive responses as sufficient; orienting responses, even if perfectly adaptive, do not make the cut because they are not sufficiently specific (while S&C single out orienting responses, it should be pointed out that even highly specific antipredator responses, such as running into the trees in response to a leopard alarm, could be potentially adaptive to some other 'referent'). In other cases, a receiver's response might indeed be highly specific to the signal's 'referent', but if it is known that the proximate mechanisms are something other than the sorts of cognitive processes necessary for taking a signal to stand for something, then S&C would not deem it functionally referential. For example, the calls of male túngara frogs could be said, from a female receiver's perspective, to function to refer to the presence of a potential mate: their production is strongly correlated with the presence of a potential mate, and their initiation of proceptive behaviours upon receiving the signal suggests that their response is adaptive to the functional referent 'mating partner' (see Grafe, 1997). If these responses are, however, driven purely by neuroendocrine responses as has been suggested (Wilczynski & Chu, 2001), then it would seem unsound to make an argument that such signals are linguistic precursors based on the fact that they function in a similar way as certain human words or phrases (see also Scott-Phillips, *in press*).

We thus entirely agree with S&C that researchers should take these kinds of factors into account in drawing conclusions about the extent to which receivers are taking the signal to stand for something (or are attributing meaning). But by allowing for these

exceptions, S&C themselves make the point that satisfaction of their production and perception criteria are necessary but not sufficient for diagnosing their conception of functional reference. This results from the fact that they have defined functional reference in proximate terms (receivers take the signal to stand for something) but provided functional criteria for diagnosing it. Satisfaction of these criteria alone does not tell us what the proximate mechanisms are.

For those specifically interested in the cognitive mechanisms underpinning receiver responses, it may be important to consider a role of information in communication playing out at two distinct levels. First, information's role may play out over evolutionary time, wherein particular innate responses to particular signals have been selected because those signals reliably correlate with something relevant to receivers. In these cases, receivers can be said to respond to the signal because the signal has some informative value, but we would not say that receivers are 'attributing meaning' to the signal. Second, information can be important at the individual level wherein an individual takes a signal to be informative because, due to prior experience, it has learned that the signal reliably correlates with something in the world. It seems that S&C would agree with the importance of this distinction, but establishing the diagnostic criteria for distinguishing between these cases will not be simple.

DISTINGUISHING MEANING ATTRIBUTION FROM DECISION MAKING IS NOT A RECIPE FOR OVERINTERPRETATION

In two previous papers (Fischer, 2013; Wheeler & Fischer, 2012), we used the example of male baboons responding to or ignoring screams from females (Palombit, Seyfarth, & Cheney, 1997) to illustrate how such variation in responses can be explained as variation either in attributed meaning or in deciding how to best respond to a signal with a given attributed meaning. We argued that different males might make different decisions in how to respond to the screams, ignoring them in cases when a response would not be individually advantageous.

S&C make the correct point that in this case '[t]wo options are possible for the unresponsive males; either they also take the signal to stand for infanticide, but do not act upon it, or they do not take the signal to stand for infanticide' (p. e4). They go on to suggest that, despite the former being a potential explanation, such a conclusion goes beyond what the data tell us; by applying their production and perception criteria, we can only conclude that males that ignore the screams do not take the screams to stand for anything because the response does not fulfil their perception requirement of functional reference. In reality, whether or not the perception criterion is met in this case is somewhat subjective, as inaction is arguably a response (Levitis, Lidicker, & Freund, 2009; see also Fischer & Hammerschmidt, 2001), and in this case would be one that is perfectly adaptive since the costs of coming to the aid of an unrelated infant would probably outweigh any benefits for the males.

The subjectivity of the perception criteria notwithstanding, are S&C correct that the fact that 'responsive males take the signal to stand for infanticide is not a reason to lean one way or the other with respect to unresponsive males'? If we are to take only the information that some males respond and others do not, we would clearly not have sufficient evidence that the unresponsive males are attributing a similar meaning as the responsive males, and that the differences in their responses are due to differences at the level of decision making. But we do have more information available to us. Of particular importance, the unresponsive males and the responsive males are the same individuals; a male that responds to the screams of his friend when she has an infant ignores those of nonfriends with infants. Because these males have the same

information available to them in both cases, and thus the same potential to attribute meaning, we believe the best interpretation is that males are varying their decision making and not their attributed meaning. But, again, one must take into account a wider range of information than only whether or not the production and perception criteria are met. Indeed, the best interpretation of the baboon example will make use of not only the full range of data available from that particular study's test and control conditions, but also other studies with baboons, and even studies of other closely related taxa. Relying only on S&C's modified production and perception criteria simply does not open enough doors for one to draw a fully informed conclusion.

Even when taking into account this wider range of data, it is clear that S&C are correct that our preferred interpretation is not the only possible interpretation. It is less clear why S&C see one type of error in interpretation (meaning attribution when it is not occurring) as more 'risky' than the other type (that it is not occurring when it in fact is), and that it is preferable to lean towards the latter even if the balance of evidence favours the former. We find it especially strange that S&C see this 'risk' as so severe that they suggest to work within a framework that does not even allow for consideration of this interpretation, even though our suggested framework allows for both interpretations, including the one that they prefer. Our framework is fruitful precisely because it sets up the different interpretations and encourages further studies, if necessary, to distinguish conclusively between these possibilities (Wheeler & Hammerschmidt, 2013).

MOVING ON

In summary, although we welcome the lively debate that is likely to move the field further, we would maintain that our framework holds up to the criticism of S&C, and that it continues to generate productive questions in the realm of animal communication and cognition. Furthermore, we believe that the revised definition presented by S&C does little to rescue the concept of functional reference. Instead, it lays bare some of the fundamental weaknesses that have been identified over the years. We therefore believe that maintaining the concept would come at the cost of luring scholars to believe that they are contributing to the understanding of the evolution of language, when they are not, and distracting researchers from more interesting questions regarding the ecology and evolution of signalling behaviour at a more general level.

Acknowledgments

We thank Andrea Scarantino, Zanna Clay, James Higham and members of the Cognitive Ethology Lab for lively and friendly discussion.

References

- Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer.
- Carazo, P., & Font, E. (2010). Putting information back into biological communication. *Journal of Evolutionary Biology*, 23, 661–669.
- Deacon, T. W. (1997). *The symbolic species: The coevolution of language and the brain*. New York, NY: W.W. Norton.
- Fedurek, P., & Slocombe, K. E. (2011). Primate vocal communication: a useful tool for understanding human speech and language evolution? *Human Biology*, 83, 153–173.
- Fischer, J. (2013). Information, inference and meaning in primate vocal communication. In U. Stegmann (Ed.), *Animal communication theory: Information and influence*. Cambridge, U.K.: Cambridge University Press.
- Fischer, J., & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition*, 4, 29–35.

- Fitch, W. T. (2010). *The evolution of language*. Cambridge, U.K.: Cambridge University Press.
- Grafe, T. U. (1997). Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. *Animal Behaviour*, 53, 1103–1117.
- Grice, H. P. (1957). Meaning. *Philosophical Review*, 66, 377–388.
- Levitis, D. A., Lidicker, W. Z., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*, 78, 103–110.
- Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, 93, 177–197.
- Manser, M. B. (2013). Semantic communication in vervet monkeys and other animals. *Animal Behaviour*, 86, 491–496.
- Marler, P. (1984). Animal communication: affect or cognition? In K. R. Scherer, & P. Ekman (Eds.), *Approaches to emotion* (pp. 345–365). Hillsdale, NJ: L. Erlbaum.
- Marler, P., Evans, C. S., & Hauser, M. D. (1992). Animal signals: motivational, referential, or both? In H. Papoušek, U. Jürgens, & M. Papoušek (Eds.), *Nonverbal vocal communication: Comparative and developmental approaches* (pp. 66–86). Cambridge, U.K.: Cambridge University Press.
- Maynard Smith, J., & Harper, D. (2003). *Animal signals*. Oxford, U.K.: Oxford University Press.
- Owren, M. J., & Rendall, D. (2001). Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology*, 10, 58–71.
- Palombit, R., Seyfarth, R., & Cheney, D. (1997). The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour*, 54, 599–614.
- Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour*, 78, 233–240.
- Ruxton, G., & Schaefer, H. (2011). Resolving current disagreements and ambiguities in the terminology of animal communication. *Journal of Evolutionary Biology*, 24, 2574–2585.
- Ryan, M. J. (1990). Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, 7, 157–195.
- Scarantino, A. (2010). Animal communication between information and influence. *Animal Behaviour*, 79(6), e1–e5.
- Scarantino, A. (2013). Rethinking functional reference. *Philosophy of Science*, 80, 1006–1018.
- Scarantino, A., & Clay, Z. (2015). Contextually variable signals can be functionally referential. *Animal Behaviour*, 100, e1–e8.
- Scott-Phillips, T. C. (2008). Defining biological communication. *Journal of Evolutionary Biology*, 21, 387–395.
- Scott-Phillips T.C. (in press). Non-human primate communication, pragmatics, and the origins of language. *Current Anthropology*.
- Seyfarth, R. M., & Cheney, D. L. (2003). Signalers and receivers in animal communication. *Annual Review of Psychology*, 54, 145–173.
- Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour*, 80, 3–8.
- Smith, W. J. (1981). Referents of animal communication. *Animal Behaviour*, 29, 1273–1275.
- Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: the past, present and the future. *Ethology*, 119, 1–11.
- Wharton, T. (2003). Natural pragmatics and natural codes. *Mind & Language*, 18, 447–477.
- Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: a promising paradigm whose time has passed. *Evolutionary Anthropology*, 21, 195–205.
- Wheeler, B. C., & Hammerschmidt, K. (2013). Factors underpinning receiver responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it counterdeception? *American Journal of Primatology*, 75, 715–725.
- Wilczynski, W., & Chu, J. (2001). Acoustic communication, endocrine control, and the neurochemical systems of the brain. In M. J. Ryan (Ed.), *Anuran communication* (pp. 23–35). Washington, D.C.: Smithsonian Institution Press.
- Zinner, D. P., Nunn, C. L., van Schaik, C. P., & Kappeler, P. M. (2004). Sexual selection and exaggerated sexual swellings of female primates. In P. M. Kappeler, & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 71–89). Cambridge, U.K.: Cambridge University Press.