

Original citation:

Townsend, Simon, Koski, Sonja E., Byrne, Richard W., Slocombe, Katie E., Bickel, Balthasar, Böckle, Markus, Braga Goncalves, Ines, Burkart, Judith M., Flower, Tom, Gaunet, Florence et al.. (2016) Exorcising Grice's ghost : an empirical approach to studying intentional communication in animals. *Biological Review*.

Permanent WRAP URL:

<http://wrap.warwick.ac.uk/80149>

Copyright and reuse:

The Warwick Research Archive Portal (WRAP) makes this work by researchers of the University of Warwick available open access under the following conditions. Copyright © and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable the material made available in WRAP has been checked for eligibility before being made available.

Copies of full items can be used for personal research or study, educational, or not-for profit purposes without prior permission or charge. Provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

Publisher's statement:

"This is the peer reviewed version of the following article: Townsend, Simon, Koski, Sonja E., Byrne, Richard W., Slocombe, Katie E., Bickel, Balthasar, Böckle, Markus, Braga Goncalves, Ines, Burkart, Judith M., Flower, Tom, Gaunet, Florence et al.. (2016) Exorcising Grice's ghost : an empirical approach to studying intentional communication in animals. *Biological Review*. which has been published in final form at <http://doi.org/10.1111/brv.12289> This article may be used for non-commercial purposes in accordance with [Wiley Terms and Conditions for Self-Archiving](#)."

A note on versions:

The version presented here may differ from the published version or, version of record, if you wish to cite this item you are advised to consult the publisher's version. Please see the 'permanent WRAP URL' above for details on accessing the published version and note that access may require a subscription.

For more information, please contact the WRAP Team at: wrap@warwick.ac.uk



Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals

Journal:	<i>Biological Reviews</i>
Manuscript ID	BRV-07-2015-0142.R3
Manuscript Type:	Original Article
Date Submitted by the Author:	18-May-2016
Complete List of Authors:	Townsend, Simon; University of Zurich, Institute for Evolutionary Biology and Environmental Studies Koski, Sonja; University of Zurich, Anthropology Institute and Museum; University of Helsinki, Center of Excellence in Intersubjectivity in Interaction Byrne, Richard; St Andrews University, School of Psychology and Neuroscience Slocombe, Katie; University of York, School of Psychology Bickel, Balthasar; University of Zurich, Department of Comparative Linguistics Braga Goncalves, Ines; University of Zurich, Institute for Evolutionary Biology and Environmental Studies Boeckle, Markus; Danube University, Department of Psychotherapy and Biopsychosocial Health Burkart, Judith; University of Zurich, Anthropology Institute and Museum Flower, Tom; University of Cape Town, Percy Fitzpatrick Institute Gaunet, Florence; Aix-Marseille University/CNRS, Laboratoire de Psychologie Cognitive Glock, Hans; University of Zurich, Institute of Philosophy Gruber, Thibaud; University of Neuchatel, Cognitive Biology Jansen, David; University of Zurich, Institute for Evolutionary Biology and Environmental Studies Liebal, Katja; Free University of Berlin, Department of Education and Psychology Linke, Angelika; University of Zurich, German Seminar Miklosi, Adam; Eotvos Lorán University, Department of Ethology van Schaik, Carel; University of Zurich, Anthropology Institute and Museum Stoll, Sabine; University of Zurich, Department of Comparative Linguistics Vail, Alex; University of Cambridge, Zoology Department Waller, Bridget; Portsmouth University, Department of Psychology Wild, Markus; University of Basel, Philosophy Seminar Zuberbühler, Klaus; University of Neuchatel, Cognitive Biology Manser, Marta; University of Zurich, Institute for Evolutionary Biology and Environmental Studies
Keywords:	communication, language evolution, intentionality, vocalisation, gesture

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



SCHOLARONE™
Manuscripts

For Review Only

1
2
3 **1 Exorcising Grice's ghost: an empirical approach to studying intentional**
4
5
6 **2 communication in animals**
7
8
9
10
11

12 Simon W. Townsend^{1,2,*}, Sonja E. Koski^{3,4}, Richard W. Byrne⁵, Katie E. Slocombe⁶,
13
14 Balthasar Bickel⁷, Markus Böckle⁸, Ines Braga Goncalves¹, Judith M. Burkart³, Tom
15
16 Flower⁹, Florence Gaunet¹⁰, Hans Johann Glock¹¹, Thibaud Gruber¹², David A.W.A.M.
17
18 Jansen¹, Katja Liebal¹³, Angelika Linke¹⁴, Adam Miklosi¹⁵, Richard Moore¹⁶, Carel P.
19
20 van Schaik³, Sabine Stoll⁷, Alex Vail¹⁷, Bridget Waller¹⁸, Markus Wild¹⁹, Klaus
21
22 Zuberbühler¹² and Marta B. Manser¹
23
24
25
26
27
28

29 ¹*Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, 8057,*
30
31 *Switzerland*

32
33 ²*Department of Psychology, University of Warwick, Coventry, CV4 7AL, UK*

34
35 ³*Anthropology Institute and Museum, University of Zurich, Zurich, 8057, Switzerland*

36
37 ⁴*Centre of Excellence in Intersubjectivity in Interaction, University of Helsinki, Helsinki, P.O. Box 4*
38
39 *00014, Finland*

40
41 ⁵*School of Psychology and Neuroscience, St Andrews University, St Andrews, KY16 9JP, UK*

42
43 ⁶*School of Psychology, University of York, York YO10 DD, UK*

44
45 ⁷*Department of Comparative Linguistics, University of Zurich, Zurich, 8032, Switzerland*

46
47 ⁸*Department for Psychotherapy and Biopsychosocial Health, Danube University, Krems, 3500,*
48
49 *Austria*

50
51 ⁹*Percy Fitzpatrick Institute, University of Cape Town, Rondebosch, 7701, South Africa*

52
53 ¹⁰*Laboratoire de Psychologie Cognitive, Aix-Marseille University/CNRS, Marseille, 13331, France*
54
55
56
57
58
59
60

- 1
2
3 24 ¹¹*Institute of Philosophy, University of Zurich, Zurich, 8044, Switzerland*
- 4
5 25 ¹²*Comparative Cognition, Institute of Biology, University of Neuchatel, Neuchatel, 2000, Switzerland*
- 6
7 26 ¹³*Department of Education and Psychology, Free University of Berlin, Berlin, 14195, Germany*
- 8
9
10 27 ¹⁴*German Seminar, University of Zurich, Zurich, 8001, Switzerland*
- 11
12 28 ¹⁵*Department of Ethology, Eötvös Loránd University, Budapest, 1117, Hungary*
- 13
14 29 ¹⁶*Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, 10117, Germany*
- 15
16 30 ¹⁷*Zoology Department, University of Cambridge, Cambridge, CB2 3EJ, UK*
- 17
18 31 ¹⁸*Department of Psychology, Portsmouth University, Portsmouth, P01 2UP, UK*
- 19
20 32 ¹⁹*Philosophy Seminar, Basel University, Basel, 4051, Switzerland*

21
22
23
24
25 33

26 34 *Author for correspondence (Simon.W.Townsend@Warwick.ac.uk).

27
28
29 35

30 36 ABSTRACT

31
32 37 Language's intentional nature has been highlighted as a crucial feature distinguishing it from other
33
34 38 communication systems. Specifically, language is often thought to depend on highly structured
35
36 39 intentional action and mutual mindreading by a communicator and recipient. Whilst similar abilities in
37
38 40 animals can shed light on the evolution of intentionality, they remain challenging to detect
39
40 41 unambiguously. We revisit animal intentional communication and suggest that progress in identifying
42
43 42 analogous capacities has been complicated by (i) the assumption that intentional (that is, voluntary)
44
45 43 production of communicative acts requires mental-state attribution, and (ii) variation in approaches
46
47 44 investigating communication across sensory modalities. To move forward, we argue that a framework
48
49 45 fusing research across modalities and species is required. We structure intentional communication into
50
51 46 a series of requirements, each of which can be operationalised, investigated empirically, and must be
52
53 47 met for purposive, intentionally communicative acts to be demonstrated. Our unified approach helps
54
55
56
57
58
59
60

1
2
3 48 elucidate the distribution of animal intentional communication and subsequently serves to clarify what
4
5 49 is meant by attributions of intentional communication in animals and humans.
6
7
8

9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31

51 *Key words:* communication, language evolution, intentionality, vocalisation, gesture.
52

53

54 CONTENTS

55 I. Introduction

56 II. The new framework

57 III. An example of intentionality in vocal communication assessed with the proposed criteria

58 IV. Conclusions

59 V. Acknowledgements

60 VI. References

61

62 **I. INTRODUCTION**

63 Language is considered to be one of the pinnacles of human biological evolution (Fitch, 2010). Its
64 emergence in the *Homo* lineage was presumably enabled by the presence of a set of cognitive abilities
65 and ecological conditions not shared by other species. One candidate for these abilities is the capacity
66 to act with, and understand, communicative intentions. The philosopher of language, Paul Grice (1957,
67 1982), was pivotal in highlighting the importance of such a psychological framework for
68 communication and many authors working in the ‘Gricean’ tradition have followed him in arguing
69 that the ability for intentional communication requires a sophisticated, pre-existing, metapsychological
70 framework in which speaker and hearer (or signaller and receiver) mutually understand one another’s
71 intentions and beliefs (Sperber & Wilson, 1995; Sperber, 2000; Tomasello, 2008; Scott-Phillips,
2015b).

1
2
3 72 Within Grice's influential analysis of speaker meaning there exist three clauses (Strawson, 1964;
4
5 73 Jacob, 1997), the conjunction of which form the basis for Grice's theory of communication. For a
6
7 74 signaller, S, to mean something *via* utterance *x* requires that: (i) S intends that S's utterance of *x*
8
9 75 induces a response, *r*, in receiver, R; (ii) S intends that R recognises that S has intention (i), and (iii) S
10
11 76 intends that R's recognition of S's intention functions at least partly in the motivation for R's response,
12
13 77 *r*. By this account, we not only intend to influence the receiver (through the production of a stimulus)
14
15 78 when communicating, we also want them to recognise that we are acting with such intentions, and
16
17 79 respond on the basis of recognising this. In linguistic pragmatics this communication of intention
18
19 80 (surmised by these three clauses) is often referred to as ostensive or Gricean communication and the
20
21 81 reiterated mutual perspective-taking that underlies this process has consequently been highlighted as a
22
23 82 defining feature of human linguistic communication (e.g. Grice, 1982; Dennett, 1983; Sperber &
24
25 83 Wilson, 1995; Sperber, 2000; Tomasello, 2008; Scott-Phillips, 2015*b*).

26
27 84 Given the proposed centrality of Gricean characterisations of communication (Grice, 1957) to human
28
29 85 communicative interaction, questions have been raised as to the uniqueness of these aspects of human
30
31 86 language. The extent to which human and non-human animal communication could involve the same
32
33 87 underlying psychological framework has been debated (Gómez, 1994; Tomasello, 2008; Scott-Phillips,
34
35 88 2015*a, b*; Moore, 2015*a*). One reason for this is that on standard accounts (Dennett, 1983; Sperber,
36
37 89 2000), Gricean communication requires that communicators are capable of entertaining very complex
38
39 90 metarepresentations – that is, representations of others' mental states. Dennett (1983, 1988) played a
40
41 91 critical role in initial attempts to operationalise animals as intentional systems by differentiating
42
43 92 between various orders of the metarepresentational complexity that intentional communication
44
45 93 requires, based on Grice's analysis (Dennett, 1983). Zero-order intentionality attributes no mentality
46
47 94 or intention to the communicative signalling of animals. First-order intentionality requires that the
48
49 95 signaller intends to signal to produce a response in the recipient, but does not require that the recipient
50
51 96 recognise this. Second-order intentionality involves complementing the intention to signal with the
52
53
54
55
56
57
58
59
60

1
2
3 97 attribution of mental states (by the recipient to the signaller); whilst third-order intentionality requires
4
5 98 that the signaller intend for the recipient to attribute to her the intention to signal. Finally, fourth-order
6
7 99 intentionality requires that signaller and recipient, alike, represent both the signaller's goal and her
8
9
10 100 intention that the recipient recognise that goal (Dennett, 1983; Sperber & Wilson, 1995; Scott-Phillips,
11
12 101 2015a, b).

13
14 102 Although this operationalisation would appear to serve as a useful guide to identifying what type of
15
16 103 intentionality an animal communicative system displays, it has also generated problems related to
17
18 104 what the levels of intentionality represent. As Dennett (1983) has noted, both first and higher orders of
19
20 105 intentionality require that an act of signalling is produced voluntarily and in a goal-directed way.
21
22
23 106 However, second-order intentionality (and beyond) likely employs cognitive mechanisms of a
24
25 107 qualitatively different kind – since it requires that both signaller and recipient engage in some form of
26
27 108 mental-state attribution. For this reason, second-order intentionality has received most interest because
28
29 109 it has been generally considered as more 'human' or, as Grice highlighted, as more indicative of 'true'
30
31 110 linguistic communication (Grice, 1957) and hence a step further along the continuum towards human
32
33 111 language (Scott-Phillips, 2015b). One major consequence is that it has since become commonplace to
34
35 112 assume that in order to demonstrate convincing evidence that animal vocal production is intentional
36
37 113 and thus relevant to human language, at the very least, an attribution of mental states during vocal
38
39 114 communication is required.

40
41
42
43 115 This emphasis of mental-state attribution is unhelpful for two reasons. Firstly, whilst adult humans are
44
45 116 competent at reiterated mental-state attribution, there is evidence that younger children find high
46
47 117 orders of metarepresentation difficult (Wimmer & Perner, 1983; Liddle & Nettle, 2006). Some
48
49 118 workers in primate cognition have therefore argued that, if standard interpretations of Grice are right,
50
51 119 then Gricean communication would be too difficult for both animals and human children. If this is
52
53 120 correct, then standard interpretations must overstate the cognitive pre-requisites of Gricean
54
55
56 121 communication (Gómez, 1994; Moore 2014, 2015a, b) – and human and animal communication may
57
58
59
60

1
2
3 122 share a common psychological framework after all. The less-intellectualised approaches to human
4
5 123 communication are supported by the argument that even in adults, speech production and
6
7 124 interpretation seems not always to require inference computation or belief ascription about speaker
8
9 125 intentions (Millikan, 1984). Furthermore, experimental studies under controlled conditions have
10
11 126 repeatedly demonstrated that mindreading is not deployed automatically during social and
12
13 127 communicative situations (Keysar, Lin & Barr, 2003; Apperly *et al.*, 2006) and is even sometimes
14
15 128 impeded by the surrounding social environment (McClung, Jentsch & Reicher, 2013).
16
17 129 A second reason for resisting the mental-state attribution approach is that it risks obscuring the goals
18
19 130 of comparative psychology and biology. The comparative approach does not aim to show that animals
20
21 131 communicate in a way that fully equates to human communication; instead it aims to elucidate
22
23 132 evolutionary precursors of crucial components of human language (Seyfarth, Cheney & Marler, 1980;
24
25 133 Zuberbühler, 2005). The comparative study of semantics, for example, does not hinge on the
26
27 134 discovery of symbolic conventions, displaced in time and space from the referents of communicative
28
29 135 behaviour (Tomasello, 2008). In that case, to try to evaluate what other animals are doing by human
30
31 136 standards is to risk failing to do justice to their abilities. A more theory-neutral approach to studying
32
33 137 intentional communication would therefore be better.
34
35
36
37
38 138 In line with this idea, over the last ten years various authors have taken a less theory-laden approach to
39
40 139 intentionality. This approach sidesteps the requirement that intentional communication involves
41
42 140 understanding the minds of others and does not assume that intentional use of communicative signals
43
44 141 involves the sorts of ‘ostensive-inferential’ communication that thinkers in the Gricean tradition have
45
46 142 argued characterises human communication. Through borrowing behavioural markers implemented by
47
48 143 developmental psychologists to distinguish between reflexive and more intentional gestural
49
50 144 communication in children (Bates *et al.*, 1979), progress has been made in identifying traits that are
51
52 145 precursors to distinctively human intentional communication systems (Leavens, Russell & Hopkins,
53
54 146 2005; Liebal, Pika & Tomasello, 2006). In a similar way to humans, non-human primates, primarily
55
56
57
58
59
60

1
2
3 147 great apes, also communicate with each other by gesturing. Observations of the production of gestures
4
5 148 suggest that they fulfil a number of the criteria specified for intentionality in communicative signals
6
7 149 (Table 1). Individuals have, for example, been observed to take into account the attention state of the
8
9 150 receiver, only gesturing when selected receivers are appropriately attentive (Leavens *et al.*, 2005), and
10
11 151 to elaborate or change the signal if their initial signal fails to reach the apparent goal (Cartmill &
12
13 152 Byrne, 2007). By avoiding the question of mental-state attribution, and by focusing on behavioural
14
15 153 markers of flexible and goal-directed communication, an array of studies have demonstrated first-
16
17 154 order intentionality in the communication of our closest living relatives (Call & Tomasello, 2007; Pika
18
19 155 & Liebal, 2012; Byrne, 2016).
20
21
22 156 However, some variation exists in the criteria of intentionality that individual studies apply to gestural
23
24 157 signals and there have been few attempts to apply all criteria to a single signal in a study species (but
25
26 158 see Leavens, Hopkins & Thomas, 2004). Moreover, each individual marker of intentionality in
27
28 159 isolation can be explained through lower-level mechanisms, without needing to invoke intentionality.
29
30 160 For example, sensitivity to the attention state of the receiver could simply be a learned discrimination
31
32 161 where signals are only produced when a receiver's face can be seen; persistence of a signal may have
33
34 162 nothing to do with an intention to communicate with an as yet unresponsive receiver, but simply that
35
36 163 signal production is emotionally driven and only when the goal is met does the underlying emotion
37
38 164 change and terminate signal production (Liebal *et al.*, 2013; Gaunet & Massiou, 2014; Savalli, Ades
39
40 165 & Gaunet, 2014). Therefore, it is important, before invoking first-order intentionality, to demonstrate
41
42 166 convergent evidence from a number of markers of intentionality for the same signal and species
43
44 167 (Liebal *et al.*, 2013; although see Vail, Manica & Bshary, 2013). Although multiple cases of
45
46 168 converging evidence do not amount to a proof, the probability of a behaviouristic explanation
47
48 169 decreases.
49
50
51
52 170 Whilst gestural studies highlight potential phylogenetic precursors to the intentional communication of
53
54 171 humans and provide crucial comparative data, similar evidence from vocal communication studies has
55
56
57
58
59
60

1
2
3 172 not been considered as equally convincing. Despite numerous attempts, researchers have failed to
4
5 173 teach enculturated apes to produce spoken language (Yerkes & Yerkes, 1929; Hayes, 1951). As their
6
7 174 vocalisations are commonly produced in specific contexts, it has been traditionally assumed that
8
9 175 vocalisations are the product of low-level emotional processes and are best characterised as
10
11 176 involuntary responses to specific stimuli rather than voluntary, goal-directed signals (Dennett, 1983;
12
13 177 Notman & Rendall, 2005; Tomasello, 2008). Furthermore, invasive procedures have shown that call
14
15 178 initiation in monkeys is mediated by limbic rather than cortical structures in the brain (Jürgens, 1992).
16
17 179 On the other hand, some studies suggest that vocal and non-vocal sounds are used intentionally. Great
18
19 180 apes use voiced and unvoiced sounds in a controlled manner that implies flexibility and intentionality
20
21 181 (Russell *et al.*, 2005; Hopkins, Taglialatela & Leavens, 2007, 2011; Hostetter *et al.*, 2007). More
22
23 182 recent studies, under natural conditions, have provided additional support for intentionality in ape
24
25 183 vocalisations (Crockford *et al.*, 2012; Crockford, Wittig & Zuberbühler, 2015; Schel *et al.*, 2013).
26
27 184 Moreover, multiple studies have shown vocalisations to be dependent on the surrounding social
28
29 185 audience in a variety of species (Marler, Dufty & Pickert, 1986; Zuberbühler, 2008; Crockford *et al.*,
30
31 186 2012). These so called ‘audience effects’ are not solely due to simple, arousal-mediated, social
32
33 187 facilitation effects (Zajonc, 1965), as might be the case when examining the presence or absence of
34
35 188 conspecifics (Tomasello, 2008). Instead, they incorporate more subtle social and behavioural
36
37 189 variations, e.g. relationship quality (Slocombe *et al.*, 2010; Schel *et al.*, 2013; Kalan & Boesch, 2015)
38
39 190 or response of receivers (Wich & de Vries, 2006).
40
41 191 Despite this body of data, the existence of intentional vocal communication in animals is still disputed
42
43 192 (Tomasello, 2008). Given the central role intentionality plays in human language and the apparent
44
45 193 disparity between the intentional production of gestures and non-intentional vocalisations in non-
46
47 194 human primates, it has been argued that language must have evolved *via* a gestural, rather than a vocal,
48
49 195 route (Corballis, 2002; Tomasello, 2008). This theoretical reasoning certainly adds fuel to the fiery
50
51 196 debate surrounding language’s evolutionary emergence. But unfortunately it fails to consider the fact
52
53
54
55
56
57
58
59
60

1
2
3 197 that the researchers working with gestures and vocalisations, respectively, are operating from different
4
5 198 bases (Slocombe, Waller & Liebal, 2011). Animal vocal communication researchers are investigating
6
7 199 how the production of vocalisations may or may not be used to influence the mental states of receivers,
8
9 200 often with negative results (Rendall, Cheney & Seyfarth, 2000; but see Crockford *et al.*, 2012; Schel *et*
10
11 201 *al.*, 2013). By contrast, gestural communication researchers are using an in-place suite of behaviours,
12
13 202 derived from child developmental work, to address how goal-directed and hence intentional (Dennett's
14
15 203 first-order intentionality) gestural production is, predominantly in primates. This means that the
16
17 204 research into vocalisations tacitly employs a more demanding criterion for intentionality than the
18
19 205 research into gestures. As a result, comparing intentional production of animal signals at different
20
21 206 levels in the two different modalities commits the mistake of not comparing like with like, and hence
22
23 207 renders it difficult to draw reliable conclusions about differences in intentionality across these
24
25 208 modalities.

26
27
28
29 209 To resolve these conceptual and methodological difficulties we propose to 'level the playing field'
30
31 210 with an updated framework in which the intentional nature of animal communication, irrespective of
32
33 211 modality, can be operationalised and systematically assessed. A single-framework approach will
34
35 212 facilitate direct comparative work amongst species and communicative mediums, providing a more
36
37 213 holistic picture of the evolution of human intentional communication.
38
39
40
41
42

43 215 **II. THE NEW FRAMEWORK**

44
45 216 The framework that we propose consists of three distinct criteria, each of which needs to be met by a
46
47 217 signal type before intentionality is ascribed to it. We do not abandon consideration of cognitive
48
49 218 components to intentionality, but instead argue that questions about whether or not vocal
50
51 219 communication is produced voluntarily and in a goal-directed way can be answered independently of
52
53 220 questions about whether the signaller and receiver are engaged in mindreading. Therefore, we return
54
55 221 to goal-directedness and its role in intentional behaviour as the first criterion requiring satisfaction.
56
57
58
59
60

222

Animal **S** intentionally communicates **I** to receiver **R** if the following three propositions all hold:

224

(1) *S acts with a goal with the content I*

Goal-directed behaviour has been a central focus of comparative psychology research over the last

three decades. At a more rudimentary level the notion of goal-direction involves the role of motor

processes organising action towards physical targets (Kenward *et al.*, 2009). However, goal-

directedness has also been implicated in intentional behaviour, as opposed to automatic or habitual

behaviour (Heyes & Dickinson, 1990). Here it is necessary to show that the goal-directed behaviour is

based upon knowledge of the relationship that exists between the action and its consequences (Wit &

Dickinson, 2009). Hence within our new framework we shift the cognitive emphasis to demonstrating

that communication is goal-directed.

Whilst we appreciate that operationalisation of goal-directedness is not straightforward, it is a far more

tangible and relevant criterion than the demonstration of mental-state attribution. Previous studies

probing the intentionality of primate gestures have emphasised the role of persistence and elaboration

in identifying goal-directedness. In line with this, we argue that goal-directedness can be empirically

investigated more generally by merging these criteria with the identification and application of

'stopping rules' (Burkart, Roelli & Richiger, 2015). When a signaller possesses a goal for its

communication, it would stop upon reaching the goal, but persist and/or elaborate the signal when the

goal is not reached (Leavens *et al.*, 2005). Thus, as with any other behavioural data, regular and

reliable observations fulfilling the criteria (e.g. a goal-dependent cessation of communication, or

indeed persistence and elaboration in the absence of the goal being met) are critical to demonstrating

the presence of a goal, causally linked with the signal. Furthermore, experimental manipulation of goal

end states leading to premature or delayed goal accomplishment is an additional, complementary way,

to assess the causal link between the goal and the communicative signal.

1
2
3 247
4
5 248
6
7 249
8
9 250
10
11 251
12
13 252
14
15 253
16
17 254
18
19 255
20
21 256
22
23 257
24
25 258
26
27 259
28
29 260
30
31 261
32
33 262
34
35 263
36
37 264
38
39 265
40
41 266
42
43 267
44
45 268
46
47 269
48
49 270
50
51
52
53
54
55
56
57
58
59
60

(2) *S produces voluntary, recipient-directed signals as a means to reach the represented goal*

We agree with Leavens *et al.* (2004) and Moore (2015b) that to show intentionality, behaviour must be under volitional control and recipient-directed. Criteria generated from studies of intentional communication in infants (Bates *et al.*, 1979) represent a valuable set of measures to address these conditions (see Table 1). One indicator of voluntary control is selective use of the signal, and in particular, selectively producing or withholding a signal in response to social factors such as audience composition and behaviour (social use). As we highlighted above, social context could in principle be part of a complex stimulus to which an automatic, innate signal-production mechanism responds. Thus Hurford (2007, p. 232) argues that only if “circumstances under which calls are given are too implausibly complex to be hardwired into the genes” should we infer that these signals are voluntary. Indicators of the recipient-directed nature of a signal include social use, audience checking and sensitivity to attentional state (Ristau, 1991; Povinelli *et al.*, 2003; Liebal, Call & Tomasello, 2004; Leavens *et al.*, 2005; Schel *et al.*, 2013). Every signal type and study species is different. So, whilst it has been suggested that the more criteria satisfied the greater the confidence that a signal is indeed intentional (Schel *et al.*, 2013), this may not always be plausible (e.g. certain criteria apply only to the visual domain). Thus we would argue for a strict *a priori* selection procedure of criteria to ensure fair comparisons across species and modalities.

(3) *S's signalling behaviour changes the behaviour of R in ways conducive to realising I*

As the last condition for intentionality, we focus on the behaviour of the receiver with respect to the signal produced. Given our shift of focus away from signaller or receiver mental-state attribution we only require that the communicative behaviour of the signaller elicits a change in the behaviour of the receiver. To rule out the pitfall of simply treating any behavioural change in the receiver as sufficient

1
2
3 271 for intentionality, we strengthen our condition by specifying that the change in the receiver's
4
5 272 behaviour must be repeatable, consistent and in line with the apparent intentions of the signaller.
6
7 273 In order to demonstrate how our conditions can be operationalised, we below interpret data from a
8
9
10 274 recent study on the alarm-calling behaviour of chimpanzees within the new framework and assess its
11
12 275 intentionality.

13 276

16 277 **III. AN EXAMPLE OF INTENTIONALITY IN VOCAL COMMUNICATION ASSESSED**
17
18 278 **WITH THE PROPOSED CRITERIA**

20 279 In a similar way to many primate and non-primate species, chimpanzees (*Pan troglodytes*
21
22
23 280 *schweinfurthii*) produce vocalisations when faced with dangerous situations (e.g. python or leopard
24
25 281 presence, inter-group interactions). However, due to the rare occurrence of such signals, experimental
26
27 282 manipulations are critical to assess rigorously the mechanisms underlying their production. Schel *et al.*
28
29 283 (2013) exposed wild chimpanzees in the Budongo Forest, Uganda, to realistic moving snake models
30
31 284 and recorded their vocal behaviour.

33
34 285 In line with our framework, it is first critical to show that signallers exposed to model snakes signal
35
36 286 with a goal with a particular content (I). To infer the goal of the signaller, Schel *et al.* (2013)
37
38 287 investigated the cessation of alarm calling in chimpanzees. Theoretically, if the goal of alarm calling is
39
40 288 to warn others, signallers should persist until all potential receivers are safe. By implementing an
41
42 289 objective behavioural criterion of 'safety' Schel *et al.* (2013) demonstrate that signal cessation was not
43
44 290 affected by the safety of the signaller, but instead occurred when receivers were safe (see also Wich &
45
46 291 de Vries, 2006). When alarm calling stopped, receivers were significantly more likely to be safe than
47
48 292 during the rest of the experimental trial.

51
52 293 Secondly, standardised criteria implemented in developmental child intentionality studies must be
53
54 294 applied to the signal to assess its voluntary nature and degree of recipient-directedness. Schel *et al.*
55
56 295 (2013) showed that the production of certain types of alarm calls is influenced by the composition of
57
58
59
60

1
2
3 296 the social audience, as the arrival of friends but not non-friends in the area elicited an increase in the
4
5 297 production of these calls. Furthermore, analysis of audience-checking behaviour, including gaze
6
7 298 alternation, suggested that signallers monitor and potentially take into account the current behaviour of
8
9 299 receivers when deciding to produce certain alarm calls. Hence chimpanzee alarm calls also appear
10
11 300 recipient-directed.

12
13
14 301 The third and final criterion requires that receivers of the signal must regularly respond in a way that is
15
16 302 in line with the signaller's presumed intentions. However, such a demonstration does not require that
17
18 303 the receivers understand and represent the intentions of the signaller; and so does not imply any
19
20 304 attribution of a mental state to the signaller by the recipient. Currently the data available from the
21
22 305 study do not sufficiently satisfy this criterion, as Schel *et al.* (2013) did not directly explore the
23
24 306 influence of alarm calling on the receiver's behaviour. Nevertheless, certain observations do suggest
25
26 307 that this condition may also have been satisfied. When hearing conspecific alarm calls, receivers have
27
28 308 been observed to behave in a similar way as when they encounter predators naturally, including
29
30 309 bipedal scanning behaviour and tree climbing (K.E. Slocombe, A. Schel, S. Townsend, Z. Machanda
31
32 310 & K. Züberbuhler, unpublished data; Crockford *et al.*, 2015; see also Cheney & Seyfarth, 1990).
33
34 311 These behavioural observations suggest that the goal of the signaller, in terms of warning group
35
36 312 members of a threat, has potentially been met. However, more systematic comparisons to baseline
37
38 313 scanning behaviour indicating that the response was caused by the communicated content are still
39
40 314 required.

41
42
43
44 315 The above example of alarm calling in chimpanzees is not designed to demonstrate intentional
45
46 316 communication. Instead, it simply serves to illustrate that the proposed framework for assessing
47
48 317 intentional communication in animals is objective and realisable. Moreover, although there have been
49
50 318 previous valuable attempts to operationalise intentionality (Leavens *et al.*, 2005; Liebal *et al.*, 2006;
51
52 319 Vail *et al.*, 2013; Hobaiter & Byrne, 2014) these have been predominantly restricted to a single
53
54 320 modality (but see Hopkins *et al.*, 2007), complicating multi-modal comparisons which are vital to
55
56
57
58
59
60

1
2
3 321 understanding intentional communication holistically. Our approach builds on existing work, but
4
5 322 crucially bridges the current gap that exists between modalities through being applicable to any
6
7 323 reliably and repeatedly observed communication signal.
8
9

10 324

11 325 **IV. CONCLUSIONS**

12
13
14 326 (1) The voluntary nature of human communication has long been considered a key, potentially unique,
15
16 327 feature of human cognition and language. In light of this, much comparative research has attempted to
17
18 328 unveil analogous or homologous forms of voluntary communication in animals as a way to understand
19
20 329 better what features are really unique to language and from this how the language faculty may have
21
22 330 evolved (Hauser, Chomsky & Fitch, 2002; Fitch, 2010). However, advances in the field have been
23
24 331 complicated by the scarcity of convincing evidence of voluntary production of animal communication
25
26 332 in the vocal domain (Wheeler & Fischer, 2012; Rendall & Owren, 2013; although see Crockford *et al.*,
27
28 333 2012). This gap in understanding has had far reaching impacts regarding the predicted evolutionary
29
30 334 route *via* which language may have evolved, namely whether the origins of language were gestural or
31
32 335 vocal.
33
34

35
36 336 (2) We propose that the problem does not lie only in insufficient data. Additionally, it is bound up
37
38 337 with a preoccupation with questions about whether voluntary communicative acts in animals are
39
40 338 produced with the same sorts of cognitively complex intentions thought characteristic of human
41
42 339 communication – in particular, the intention to modify the mental states of receivers. Although
43
44 340 mental-state attribution and its role in mediating signal production is an important component of
45
46 341 human intentional communication (Dennett, 1983; Crockford *et al.*, 2012), we argue that focusing on
47
48 342 this alone detracts from equally informative examples of behaviour. Moreover, the assumption that
49
50 343 human communication must aim at changing mental states has been challenged (Moore, 2015a).
51
52

53
54 344 (3) How widely distributed first-order intentionality is across the animal kingdom is a key question
55
56 345 that must be addressed if we are to (i) understand the unique qualities of intentionality in humans, (ii)
57
58
59
60

1
2
3 346 shed light on the modality and evolutionary route *via* which language evolved, and (*iii*) understand
4
5 347 more generally the adaptive benefit of intentional signalling in non-human animals.

6
7 348 (4) Critically, we provide the necessary framework to address first-order intentionality, whether
8
9 349 analogous or homologous, across modalities and species giving rise to a unified and unbiased
10
11 350 understanding of the nature of intentional communication in animals.
12
13 351

14 352 **V. ACKNOWLEDGEMENTS**

15
16 353 This paper was seeded in a workshop “Deciphering the origins of intentional communication in
17
18 354 animals: an integrative approach” at the University of Zurich. S.W.T., S.E.K., and I.B.G. thank the
19
20 355 University of Zurich’s Graduate Campus Grant for funding the workshop. We thank the anonymous
21
22 356 reviewer for constructive and helpful comments.
23
24 357

25 358 **VI. REFERENCES**

- 26
27
28
29
30 359 APPERLY, I.A., RIGGS, K.J., SIMPSON, A., SAMSON, D. & CHIAVARINO, C. (2006). Is belief reasoning
31
32 360 automatic? *Psychological Science* **17**, 841–844.
33
34 361 BATES, E., BENIGNI, L., BRETHERTON, I., CAMAIONI, L. & VOLTERRA, V. (1979). *The emergence of*
35
36 362 *symbols: cognition and communication in infancy*. New York: Academic Press.
37
38 363 BURKART, J. M., ROELLI, C. & RICHIGER, R. (2015). When is behavior intentional? The case of
39
40 364 proactive prosociality. 6th EFP meeting, *Folia Primatologica* **86**, 253–254.
41
42 365 BYRNE, R. (2016). *Evolving Insight*. Oxford University Press.
43
44 366 CALL, J. & TOMASELLO, M. (2007). *The gestural communication of apes and monkeys*. Mahwah, New
45
46 367 York: Lawrence Erlbaum Associates.
47
48 368 CARTMILL, E. A. & BYRNE, R. W. (2007). Orangutans modify their gestural signaling according to
49
50 369 their audience's comprehension. *Current Biology* **17**, 1345–1348.
51
52 370 CHENEY, D.L. & SEYFARTH, R.M. (1990). *How monkeys see the world*. Chicago: University of
53
54
55
56
57
58
59
60

- 1
2
3 371 Chicago Press.
4
5 372 CORBALLIS, M.C. (2002). *From hand to mouth: The origins of language*. Princeton University Press,
6
7 373 Princeton NJ.
8
9 374 CROCKFORD, C., WITTIG, R. M., MUNDRY, R. & ZUBERBÜHLER, K. (2012). Wild Chimpanzees Inform
10
11 375 Ignorant Group Members of Danger. *Current Biology* **22**, 142–146.
12
13 376 CROCKFORD, C., WITTIG, R. M. & ZUBERBÜHLER, K. (2015). An intentional vocalization draws others'
14
15 377 attention: A playback experiment with wild chimpanzees. *Animal Cognition*, **18**(3), 581–591.
16
17 378 DENNETT, D.C. (1983). Intentional systems in cognitive ethology “The Panglossian paradigm”
18
19 379 defended. *Behavioral and Brain Sciences* **6**, 343–390.
20
21 380 DENNETT, D. C. (1988). Précis of The Intentional Stance. *Behavioral and Brain Sciences* **11**, 495–546.
22
23 381 FITCH, W.T.F. (2010). *The Evolution of language*. Cambridge University Press, Cambridge UK.
24
25 382 GAUNET, F. & MASSIOUI, F. (2014). Marked referential communicative behaviour, but no
26
27 383 differentiation of the “knowledge state” of humans in untrained pet dogs vs. 1-year-old infants.
28
29 384 *Animal Cognition* **17**, 1137–1147.
30
31 385 GÓMEZ, J. C. (1994). Mutual awareness in primate communication: a Gricean approach. In Parker,
32
33 386 Mitchell, & Boccia (eds.) *Self-Awareness in Animals and Humans*. Cambridge: CUP.
34
35 387 GRICE, P. (1957). Meaning. *Philosophical Review* **64**, 377–388.
36
37 388 GRICE, P. (1982). Meaning Revisited. Pages 223–243 in N.V. Smith, ed. *Mutual Knowledge*. New
38
39 389 York: Academic Press.
40
41 390 HAUSER, M. D., CHOMSKY, N. & FITCH, W.T.F. (2002). The Faculty of Language: What Is It, Who
42
43 391 Has It, and How Did It Evolve? *Science* **298**, 1569–1579.
44
45 392 HAYES, C. (1951). *The Ape in Our House*. New York: Harper.
46
47 393 HEYES, C. & DICKINSON, A. (1990). The intentionality of animal action. *Mind and Language* **5**, 87–
48
49 394 103,
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 395 HOBATER, C. & BYRNE, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology* **24**,
4
5 396 1596–1600.
6
7 397 HOPKINS, W. D., TAGLIALATELA, J. P., & LEAVENS, D. A. (2007). Chimpanzees differentially produce
8
9 398 novel vocalizations to capture the attention of a human. *Animal Behaviour*, **73**(2), 281–286.
10
11 399 HOPKINS, W. D., TAGLIALATELA, J. P., & LEAVENS, D. A. (2011). Do chimpanzees have voluntary
12
13 400 control of their facial expressions and vocalizations? In *Primate communication and human*
14
15 401 *language: Vocalisation, gestures, imitation and deixis in humans and non-humans* (pp 71–88).
16
17 402 John Benjamin Publishing Company.
18
19
20 403 HOSTETTER, A. B., RUSSELL, J. L., FREEMAN, H., & HOPKINS, W. D. (2007). Now you see me, now you
21
22 404 don't: evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition*,
23
24 405 **48**(2), 87–96.
25
26
27 406 HURFORD, J. R. (2007). *The origins of meaning: Language in the light of evolution*. Oxford University
28
29 407 Press, USA.
30
31
32 408 JACOB, P. (1997). *What minds can do*. Cambridge: Cambridge University Press.
33
34 409 JÜRGENS, U. (1992). On the neurobiology of vocal communication. In Papousek H., Jürgens U.,
35
36 410 Papousek, M., eds. *Nonverbal Vocal Communication*. (pp 3–42) Cambridge, UK: Cambridge
37
38 411 University Press.
39
40
41 412 KALAN, A. K. & BOESCH, C. (2015). Audience effects in chimpanzee food calls and their potential for
42
43 413 recruiting others. *Behavioral Ecology and Sociobiology*, **69**(10), 1701–1712.
44
45 414 KENWARD, B., FOLKE, S., HOLMBERG, J., JOHANSSON, A. & GREDEBÄCK, G. (2009). Goal-directedness
46
47 415 and decision making in infants. *Developmental Psychology* **45**, 809–819.
48
49 416 KEYSAR B., LIN S. & BARR D.J. 2003. Limits on theory of mind use in adults. *Cognition* **89**: 25–41.
50
51 417 LEAVENS, D. A., HOPKINS, W. D., & THOMAS, R. K. (2004). Referential Communication by
52
53 418 Chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **118**, 48–57.
54
55
56
57
58
59
60

- 1
2
3 419 LEAVENS, D. A., RUSSELL, J. L. & HOPKINS, W. (2005). Intentionality as measured in the persistence
4
5 420 and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development* **76**,
6
7 421 291–306.
8
9
10 422 LIDDLE, B. & NETTLE, D. (2006). Higher-order theory of mind and social competence in school-age
11
12 423 children. *Journal of Cultural and Evolutionary Psychology*, **4**(3-4), 231–244.
13
14 424 LIEBAL, K., CALL, J., & TOMASELLO, M. (2004). Use of gesture sequences in chimpanzees. *American*
15
16 425 *Journal of Primatology*, **64**(4), 377–396.
17
18 426 LIEBAL K., PIKA S. & TOMASELLO M. (2006). Gestural communication of orangutans (*Pongo*
19
20 427 *pygmaeus*). *Gesture* **6**, 1–38.
21
22
23 428 LIEBAL, K., WALLER, B. BURROWS, A. & SLOCOMBE, K. (2013). *Primate communication: a*
24
25 429 *multimodal approach*. Cambridge University Press.
26
27
28 430 MARLER P.M, DUFTY A, PICKERT R. (1986). Vocal communication in the domestic chicken: II. Is a
29
30 431 sender sensitive to the presence and nature of a receiver? *Animal Behaviour* **34**, 194–198.
31
32 432 MCCLUNG, J., JENTZSCH, I. & REICHER, S. (2013). Group Membership Affects Spontaneous Mental
33
34 433 Representation: Failure to Represent the Out-Group in a Joint Action Task. *PLoS ONE* **8**, e79178
35
36 434 MILLIKAN, R. (1984). *Language, thought and other biological categories*. Cambridge (Mass), MIT
37
38 435 Press.
39
40
41 436 MOORE, R. (2014). Ontogenetic constraints on Paul Grice's theory of communication. In Danielle
42
43 437 Matthews (ed.) *Pragmatic Development in First Language Acquisition* (pp 87–104.). Amsterdam:
44
45 438 John Benjamins Publishing Company.
46
47
48 439 MOORE, R. (2015a). A common intentional framework for ape and human communication. *Current*
49
50 440 *Anthropology*, **56**(1), 71–72.
51
52 441 MOORE, R. (2015b). Meaning and ostension in great ape gestural communication. *Animal Cognition*
53
54 442 **19**, 223–231.
55
56
57
58
59
60

- 1
2
3 443 NOTMAN, H. & RENDALL, D. (2005). Contextual variation in chimpanzee pant hoots and its
4
5 444 implications for referential communication. *Animal Behaviour*, **70**(1), 177–190.
6
7 445 PIKA, S. & LIEBAL, K. (2012). (Eds.), *Developments in Primate Gesture Research*. Amsterdam: John
8
9 446 Benjamins Publishing Company.
10
11 447 POVINELLI, D., THEALL, L., REAUX, J., DUNPHY-LELII, S. (2003). Chimpanzees spontaneously alter the
12
13 448 location of their gestures to match the attentional orientation of others. *Animal Behaviour*, **65**, 1–9
14
15 449 RENDALL, D., CHENEY, D. L. & SEYFARTH, R. M. (2000). Proximate factors mediating “contact” calls
16
17 450 in adult female baboons (*Papio cynocephalus ursinus*) and their infants. *Journal of Comparative*
18
19 451 *Psychology* **114**, 36–46.
20
21 452 RENDALL, D. & OWREN, M.J. (2013). Communication without meaning or information: abandoning
22
23 453 language-based and informational constructs in animal communication theory. In U.E. Stegmann,
24
25 454 ed. *Animal communication theory: Information and influence*, (pp 151–188). Cambridge
26
27 455 University Press, Cambridge UK.
28
29 456 RISTAU, C. (1991). Aspects of the cognitive ethology of an injury-feigning bird, the piping plover.
30
31 457 In *Cognitive Ethology: The Minds of Other Animals*, ed. C. Ristau, Lawrence Erlbaum Associates,
32
33 458 Hillsdale.
34
35 459 RUSSELL, J. L., BRACCINI, S., BUEHLER, N., KACHIN, M. J., SCHAPIRO, S. J., & HOPKINS, W. D. (2005).
36
37 460 Chimpanzee (*Pan troglodytes*) intentional communication is not contingent upon food. *Animal*
38
39 461 *Cognition*, **8**(4), 263–272.
40
41 462 SAVALLI, C., ADES, C. & GAUNET, F. (2014). Are dogs able to communicate with their owners about a
42
43 463 desirable food in a referential and intentional way? *Plos ONE* **9**, e111387.
44
45 464 SCHEL, A.M., TOWNSEND, S.W., MACHANDA, Z., ZUBERBÜHLER, K. & SLOCOMBE, K.E. (2013).
46
47 465 Chimpanzee alarm call production meets key criteria for intentionality. *PLoS ONE* **8**, e76674.
48
49 466 SCOTT-PHILLIPS, T. C. (2015a). Meaning in animal and human communication. *Animal Cognition*,
50
51 467 **18**(3), 801–805.
52
53
54
55
56
57
58
59
60

- 1
2
3 468 SCOTT-PHILLIPS, T.C. (2015b). Nonhuman primate communication, pragmatics, and the origins of
4
5 469 language. *Current Anthropology* **56**, 56–80.
6
7 470 SEYFARTH, R. M., CHENEY, D. L. & MARLER, P. (1980). Monkey responses to three different alarm
8
9 471 calls: evidence of predator classification and semantic communication. *Science* **210**, 801–803.
10
11 472 SLOCOMBE, K. E., KALLER, T., TURMAN, L., TOWNSEND, S.W., PAPWORTH, S & ZUBERBÜHLER, K.
13
14 473 (2010). Production of food-associated calls in wild chimpanzees is dependent on the composition
15
16 474 of the audience. *Behavioural Ecology and Sociobiology* **64**, 1959–1966.
17
18 475 SLOCOMBE, K. E., WALLER, B. M. & LIEBAL, K. (2011). The language void: the need for multimodality
19
20 476 in primate communication research. *Animal Behaviour* **5**: 919–924.
21
22 477 SPERBER, D. (2000). Meta-representations in an evolutionary perspective. In Sperber (ed.) *Meta-*
23
24 478 *representations: A Multidisciplinary Perspective*. Oxford: OUP.
25
26 479 SPERBER, D. & WILSON, D. (1995). *Relevance: Communication and Cognition*, Second Edition,
27
28 480 Oxford/Cambridge: Blackwell Publishers.
29
30 481 STRAWSON, P.F. (1964). Intention and convention in speech acts. *Philosophical Review* **73**, 439–460.
31
32 482 TOMASELLO, M. (2008). *Origins of Human Communication*. MIT Press.
33
34 483 VAIL, A.L., MANICA, A. & BSHARY, R. (2013). Referential gestures in fish collaborative hunting.
35
36 484 *Nature Communications* **4**, 1765 (1–7).
37
38 485 WHEELER, B. C. & FISCHER, J. (2012). Functionally referential signals: A promising paradigm whose
39
40 486 time has passed. *Evolutionary Anthropology* **21**, 195–205.
41
42 487 WICH S.A. & DE VRIES H. (2006). Male monkeys remember which group members have given alarm
43
44 488 calls. *Proceedings of the Royal Society Series B* **273**, 735–740.
45
46 489 WIMMER, H & PERNER, J. (1983). Beliefs about beliefs: representation and constraining function of
47
48 490 wrong beliefs in young children’s understanding of deception. *Cognition*, **13**, 103–128.
49
50 491 WIT, S. & DICKINSON, A. (2009). Associative theories of goal-directed behaviour: a case for animal–
51
52 492 human translational models. *Psychological Research* **73**, 463–476.
53
54
55
56
57
58
59
60

- 1
2
3 493 YERKES, R. M. & YERKES, A. W. (1929). *The great apes: a study of anthropoid life*. New Haven: Yale
4
5 494 University Press.
6
7 495 ZAJONC, R.B. (1965). Social facilitation. *Science*, **149**, 269–274.
8
9 496 ZUBERBÜHLER, K. (2005). The phylogenetic roots of language: evidence from primate communication
10
11 497 and cognition. *Current Directions in Psychological Science* **14**, 126–130
12
13 498 ZUBERBÜHLER, K. (2008). Audience effects. *Current Biology*, **18**, R190.
14
15 499
16
17 500
18
19 501
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only

1
2
3 502 Table 1. The criteria for intentional communication in animals pertinent to step 2 in the new
4
5 503 framework. Amended from Schel *et al.* (2013).
6
7 504
8
9

Criterion	Explanation	505
		506
Social use	The signal is directed at a recipient. This can be assessed at various levels: (1) Presence/absence of audience effect: the signal is only produced in the presence of a recipient. (2) Composition of audience: the signal is only produced in the presence of certain recipients (e.g. kin, dominants, friends) (3) Behaviour of audience: signal production is contingent on the behaviour of the recipient	507 508 509 510
Sensitivity to attentional state of recipient	Visual signals are only produced in the field of view of recipients. If signaller does not have a recipient's visual attention, tactile or auditory signals should be produced. This can also be considered a social use level-3 audience effect.	511 512
Manipulation of attentional state of recipient	Before a visual signal is produced, attention-getting behaviours are directed towards a recipient who is not visually attending to the signaller or the signaller moves itself into the line of view of a recipient (Liebal <i>et al.</i> , 2004).	513 514
Audience checking and gaze alternation	Signaller monitors the audience and visually orients towards the recipient before producing a signal. If a third entity is involved, gaze alternation may occur between recipients and this entity.	515 516