



A multifaceted framework to establish the presence of meaning in non-human communication

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1 **A multifaceted framework to establish the presence of meaning in**
2 **non-human communication**

3
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18
19 **ABSTRACT**

20 Does non-human communication, like language, involve meaning? This question guides our
21 focus through an interdisciplinary review of the theories and terminology used to study
22 meaning across disciplines and species. Until now, it has been difficult to apply the concept
23 of meaning to communication in non-humans. This is partly because of the varied approaches
24 to the study of meaning. Additionally, while there is a scholarly acknowledgement of
25 potential meaning in non-human cognition, there is also scepticism when the topic of

26 communication arises. We organise some of the key literature into a coherent framework that
27 can bridge disciplines and species, to ensure that aspects of meaning are accurately and fairly
28 compared. We clarify the growing view in the literature that, rather than requiring multiple
29 definitions or being split into different types, meaning is a multifaceted yet still unified
30 concept. In so doing, we propose that meaning is an umbrella term. Meaning cannot be
31 summed up with a short definition or list of features, but involves multiple complexities that
32 are outlined in our framework. Specifically, three global facets are needed to describe
33 meaning: a *Signal Meaning Facet*, an *Interactant Meaning Facet*, and a *Resultant Meaning*
34 *Facet*. Most importantly, we show that such analyses are possible to apply as much to non-
35 humans as to humans. We also emphasise that meaning nuances differ among non-human
36 species, making a dichotomous approach to meaning questionable. Instead, we show that a
37 multifaceted approach to meaning establishes how meaning appears within highly diverse
38 examples of non-human communication, in ways consistent with the phenomenon's presence
39 in human non-verbal communication and language(s). Therefore, without further recourse to
40 'functional' approaches that circumvent the critical question of whether any non-human
41 meaning exists, we show that the concept of meaning is suitable for evolutionary biologists,
42 behavioural ecologists, and others to study, to establish exactly which species exhibit
43 meaning in their communication and in what ways.

44

45 *Key words:* animal communication, communicative intentionality, functional reference,
46 language origins, meaning, non-human signals, pragmatics, reference, semantics, symbolic
47 signs.

48

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79

80 I. INTRODUCTION

81 Does non-human communication, like language, involve meaning? We argue that it does,
82 with the notable caveat that it is possible that meaning is not exhibited in all non-human
83 communication by all species, but that meaning is now investigable in all non-human
84 communication. Moreover, our multifaceted framework can be used to establish this presence
85 of non-human communicative meaning. Firstly, it is crucial to note that there is currently no
86 fixed, agreed-upon definition of meaning. It is “the sort of concept which resists definition
87 and conceptual analysis” (Glock, 2012, p. 52). The very meaning of the term *meaning* is
88 heavily context based and discipline dependent, and involves a range of terminology:
89 *meaning, semantics, semiotics, (functional) reference*, and so forth. A definition becomes
90 more complex when we factor in additional aspects, including whether scholars are
91 discussing conventional arbitrary semantics as opposed to context- and usage-based
92 pragmatics, or discussing how symbolic *versus* indexical signs operate – topics we will
93 explore in greater depth herein. Are these aspects different parts of the same phenomenon of
94 meaning, or are they different types of meaning? Moreover, which, if any, of the applications
95 of *meaning* can we attribute to non-human communication?

96 Until now, it has been difficult to apply the concept of meaning to non-humans, especially
97 their communication, partly because of the varied approaches to the study of meaning and
98 lack of the concept’s definition. Additionally, while there is some scholarly
99 acknowledgement of the relevance of meaning in non-human cognition, there is also
100 considerable scepticism when the topic of communication arises. Such scepticism comes

101 from a reluctance to assume intentionality in non-humans, and also where contentious
102 comparisons are made between language(s) and the communication systems of non-humans
103 (topics raised by Scott-Phillips, 2015). Thus, there is often recourse to ‘functional’
104 interpretations of non-human communication, such as with the proposal of ‘functional
105 reference’ (Macedonia & Evans, 1993), to acknowledge aspects consistent with human
106 communication but simultaneously to circumvent the complicated question of whether non-
107 human meaning exists. We aim to review and organise key literature in the meaning
108 landscape into a coherent framework that can bridge disciplines and species, to ensure that
109 aspects of meaning are being accurately and fairly compared. We also advance an
110 understanding of meaning by highlighting that, to study meaning, we must adopt a
111 multifaceted perspective. Our comparative framework aims to enable researchers to recognise
112 various aspects of meaning in non-human communication, a term which encompasses at least
113 hundreds of thousands of animal species other than humans (Mora *et al.*, 2011), and so
114 involves an impressive diversity that challenges a simple dichotomous human/non-human
115 perspective.

116 Our contribution is similar to Berthet *et al.*’s (2023) animal linguistics primer. We deal with
117 the same challenges of interpreting non-human communication, but we provide a more
118 expanded insight into meaning than the definition that Berthet *et al.* (2023, p. 83) propose:
119 “The set of features of circumstances that appear at a rate greater than chance across the
120 signal’s occurrences.” In doing so, we also make explicit the importance of the growing view
121 that, rather than requiring multiple definitions or being split into different types, meaning
122 should be viewed as a multifaceted concept. We outline three global facets that arise from a
123 synthesis of the literature: a *Signal Meaning Facet* pertaining to the nature of the
124 communicative signal itself, an *Interactant Meaning Facet* pertaining to the motivations and
125 inferences of the interacting communicative participants and the situational context, and a

126 *Resultant Meaning Facet* pertaining to the outcome of the communicative signal and
127 signaller-perceiver interaction, along with their theoretical basis and terminology.

128 Throughout, we also consider Tinbergen's (1963) four questions for studying animal
129 behaviour: mechanisms (causation), ontogeny (development), function (survival value), and
130 evolutionary history, and the need to explain the concept of meaning in terms of its adaptive
131 value, without which it would not have arisen at all. We also highlight recent research
132 demonstrating how non-human communication may be integrated into a concept of language
133 through the perspective of continuous rather than discrete categorisation of abstract concepts
134 like language. This inclusive approach could be extended to meaning as well. Ultimately, we
135 argue that such a combined multifaceted and continuous categorisation approach establishes
136 the justification for applying the concept of meaning to at least some instances of non-human
137 communication. This has strong implications for the study of the nature of meaning,
138 language, and non-human communication combined, as well as a richer understanding of the
139 evolutionary pathways involved.

140 In the next section, we explore the cross-disciplinary literature with a broad perspective,
141 rather than delving into nuances, to identify key themes emerging that must be integrated into
142 a theoretical framework of meaning across species. Following this review, we take
143 multifaceted theories of meaning as a basis for expanding on the main themes, and organise
144 the themes into three global facets, which are then comprehensively discussed. We add a
145 worked example of how this meaning framework can be applied to a non-human instance of
146 communication. We then make note of final supporting evidence to substantiate our approach
147 as well as our claim that the various aspects of meaning can be found in the communication
148 of many non-human species.

149 Throughout, we make use of many examples based on human experience, as the reader may
150 find the intention of the communicative act, and the perception of that act, easier to

151 understand. Moreover, it helps to elucidate the comparatively smaller repertoire of
152 documented intentional communication amongst non-humans, as well as allowing for the fact
153 that cognitive processes may differ across species, which is a flourishing area of research.
154 A final necessary caveat is the matter of terminological definitions in two respects. First, we
155 must note the complexity involved in each area of this research, each leading to its own
156 avenue of detailed debates. We have therefore adopted working definitions and examples
157 throughout to attempt to streamline these complex issues, present a single perspective on each
158 of the topics, and maintain focus on how to unify all the key concepts relating to meaning
159 into a framework that can be applied across disciplines and species. Second, we note that
160 linguistic terminology borrowed by comparative researchers may sometimes be applied to
161 other species without clear definition or description of how the concept is being
162 operationalised, so that terminology may be used differently in various studies. Again, our
163 framework assists the comparative approach to give greater consistency and clarity over
164 which aspects of meaning are being explored for a given species.

165

166 **II. THE THEMES OF MEANING**

167 This section discusses key themes that arise in the interdisciplinary literature. Firstly, there is
168 the role of mental representations, the ‘having of concepts’, which are fundamental units of
169 knowledge analysed from perceptual experience (Evans, 2007), and without which there can
170 be no meaning. This leads naturally into a discussion of reference, which connects mental
171 meaning with the world and is also the most observably meaningful part of communication,
172 our main focus here. However, a serious confound must then be addressed concerning four
173 competing ways in which the term *semantics* is used. Another prominent aspect of the study
174 of meaning – the content of meaning, which connects with our need to explain the adaptive
175 value of meaning (Tinbergen, 1963) and how it evolved – can be summed up with the

176 question: what does meaning achieve? The best-known theories ascribe to meaning the role
177 of reference, information transfer and/or influencing behaviour, and the conveying and
178 recognition of communicative intentions, which are all dealt with in separate subsections.
179 Lastly, there are theories that point to the multifaceted nature of meaning, although without
180 making the importance of this point explicit in itself. We will argue that this point is crucial
181 to a more in-depth understanding of meaning and where it can be found across species. We
182 consider five topics: mental representations, semantics, referencing information or
183 manipulating behaviour, communicative intentionality that supports such reference or
184 manipulation, and multifaceted theories of meaning. These topics provide the reader with an
185 overview of the key debates and a thematic summary of how meaning has been treated in the
186 literature so far. This establishes a firm foundation upon which our cross-species meaning
187 framework can be built.

188

189 **(1) The role of mental representations**

190 From the perspective of studying humans at least, meaning is closely related to the notion of
191 mental representations, which is how concepts intervene between perception and responses
192 and can be built from perception of the real world or other imagined/stored concepts. This
193 addresses the cognitive dimensions of meaning. This notion of mental representations and a
194 consideration of real and conceptual entities partly aligns with the semantic/pragmatic
195 distinction, which is based upon whether an actual context is involved in a
196 perceived/imagined situation. Mental representations also align with reference, which
197 requires meaning in the mind to be separated from the objects and contexts observed in the
198 real world. Thus, Frege's (1948) dualistic notion of *sense* emphasises the 'cognitive value'
199 counterpart to a hypothetical or real-world referent within meaning's *reference* (a cognitive
200 means of indication).

201 Reference is central to how meaning is signalled and/or inferred communicatively. In
202 language(s), two distinct reference strategies are considered: a *words-to-world reference*,
203 where linguistic symbols activate mental representations that are linked to actual world
204 perception and experience, and a *words-to-words reference*, which is intrinsic to the linguistic
205 system and helps to structure these mental representations for communication, at least for
206 humans. For instance, the indefinite article ‘a’ in the phrase ‘a dog’ points to nothing in the
207 real world, but rather to the generic concept of ‘dog’ (Evans, 2015, 2016). Thus, language has
208 several layers of abstraction from the real world. Hurford (2007) argues extensively in favour
209 of such an intermediary mental representation of the world in humans as the evolutionary
210 basis for semantics. In this view, semantics has evolved within human communication to
211 structure and express the already existing mental representations.

212 Hurford (2007) goes a step further and suggests that non-humans also possess mental
213 representations, as a pre-linguistic pre-semantic layer of cognition. However, this view is
214 heavily disputed, including an argument that mental representations are not even required for
215 reference to operate, which removes the need to equate non-humans with humans in this way
216 (Evans, 1997). Yet evidence for complex cognition and mental representations in other
217 animals is growing (e.g. Fitch, 2019; Ongstad, 2021). For instance, potential non-human
218 mental representations can include mental time travel by corvids caching food for future
219 consumption, for instance based upon anticipated availability, as well as keeping track of
220 what they hid in the past, where, and who was watching at the time (e.g. Clayton & Wilkins,
221 2017). Meanwhile, the literature on manipulation and deception in non-humans suggests that,
222 although more complex cognitive capacities may not be necessary, they may still be
223 involved, as explored by Courtland (2015).

224 Indeed, the notion of signalling being inherently honest without manipulation, perhaps due to
225 signalling costs of deception in evolutionary terms, is discussed both with respect to human

226 communication (e.g. Buller & Burgoon, 1996) and in the evolutionary biology literature (e.g.
227 Whiten & Byrne, 1988), in terms of the usefulness and legitimacy of a signal for signallers
228 and perceivers (e.g. Akçay *et al.*, 2013), as well as unambiguous manipulation. Early studies
229 tended to claim that only honest signalling is possible within non-human communication
230 (Rowell *et al.*, 2006). However, beyond any possible misinformation transfer or error in
231 signalling, deception may also occur in non-human communication, as a strategic interaction.
232 There are multiple acknowledged Machiavellian behaviours in the animal kingdom (e.g.
233 Byrne & Whiten, 1988; Knight, 1998), such as ‘social tool use’ in chimpanzees (*Pan*
234 *trogodytes*) that manipulate others to obtain a food source (Schweinfurth *et al.*, 2018), and
235 fork-tailed drongos (*Dicrurus adsimilis*) that utter false alarm calls to scare other animals
236 from their food source to steal it (Flower, Gribble & Ridley, 2014). These communicative
237 behaviours could fulfil the requirement of Adams & Beighley (2013) that true *prevarication*
238 is possible only after a concept of deceit has been established in the mind of the signaller,
239 which the alleged presence of mental representations in other species would support.
240 Some game theorists argue that the content or meaning of a signal derives specifically from
241 contexts of collaborative common interest (Skyrms & Barrett, 2019), and this is explicitly in
242 the form of honest signalling, even for humans. One example the authors give is that the
243 brand name ‘Louis Vuitton’ derives its meaning and societal value from ‘honest’
244 authentically made and therefore common interest/collaborative products like suitcases. The
245 meaning associated with the brand name ‘Louis Vuitton’ would hold even if most items in
246 the world bearing the name Louis Vuitton were found to be fake, because the meaning arises
247 from the honest signal, here the genuine label name. Grice’s (1975) cooperative principle also
248 describes how humans make their conversational contributions appropriate to the situation in
249 terms of four maxims: the *quantity* of information is relative to what is required, there is a
250 truthful and adequately evidenced *quality* of contributions, which are *relevant*, and are

251 contributed in a *manner* that offers clarity, brevity, and order. This principle therefore lists
252 honesty as a principle underlying effective human communication. Yet, regardless of which
253 is the more effective evolutionary strategy, deception also abounds across species, as a
254 potential indication of mental representation in humans and non-humans alike. Given the
255 strong associations between mental representation and meaning topics like reference, as well
256 as the increasing supportive evidence for mental representations in non-humans, this indicates
257 that meaning is cognitively possible for non-humans, potentially also within their
258 communication.

259

260 **(2) Reference, semantics, and pragmatics**

261 *(a) Reference and semantics*

262 The discussion of the mental representation and cognitive aspect of meaning, touching on
263 reference, leads naturally to a discussion of reference in more depth, because this is where
264 meaning connects most observably with communication. However, to move forward with the
265 literature review and the framework we are constructing, we must first discuss how semantics
266 is used. *Semantics/semanticity* can be used as a term to discuss meaning generally, and is
267 used extensively within human centric scholarship, as well as increasingly in non-human
268 communication literature (e.g. Seyfarth, Cheney & Marler, 1980; Suzuki, Wheatcroft &
269 Griesser, 2020). However, semantics is often used as a heading for its three associated
270 phenomena, which are three distinct ways in which meaning can be conveyed within and in
271 addition to a signal across species: reference or sense and referent relations (Frege, 1948), the
272 three sign forms (Peirce, 1984) – especially symbols (Saussure, 1966), and context (or more
273 specifically independence from context, as opposed to context-based *pragmatics*). We will
274 now explore these three often-conflated associations with *semantics*.

275 Firstly, semantics partially relates to reference. *Reference* concerns the ways in which words
276 and sentences relate or point to something in the mind and/or the external world (Glock,
277 2012), as with Ogden & Richard's (1946) Triangle of Reference, which explains the
278 relationship between a symbol, referent, and thought/reference. Reference may be considered
279 as one of the most intuitive ways in which people think of meaning. Reference stems from
280 Frege's (1948) distinction between the *sense* and *referent* of linguistic expressions, also
281 known as the *intension* and *extension* (Pietroski, 2017) of a concept, which relates to the
282 inward cognitive side of *sense* and the external *referent*. Frege (1948) stipulates that the
283 referent of an expression is the actual object or event that the expression refers to, while the
284 sense is the 'cognitive value' or conceptualisation corresponding to the expression through
285 which a referent is indicated. The example Frege (1948) uses is the planet Venus. Venus can
286 be called both the 'morning star' and the 'evening star.' The referent is the same in both
287 expressions, as the physical planet itself does not change, but the sense and the properties of
288 Venus that are picked out are different in the two expressions. Alternatively, the concept
289 'unicorn' has a clear internal sense but no real-world referent because unicorns remain
290 undiscovered. Therefore, *semantics* is considered not only to discuss meaning generally but
291 also the way in which to specify meanings, when seen through this perspective of
292 conventionalised reference (Hockett, 1959). Occasionally, semantics is even considered to be
293 the same concept as reference (e.g. Townsend & Manser, 2013).

294 As its second more distinct usage, *semantics* is often linked to symbolic signs too. Peirce
295 (1984) noted that there is a triadic set of forms that a sign may take: icons or 'likenesses', for
296 instance when we outline the shape of a box with our hands; indexes, in which signs in some
297 way directly correspond to real objects, like a pointed finger guiding one's attention, as with
298 African savannah elephants (*Loxodonta africana*) guided to food (Smet & Byrne, 2013); and
299 lastly symbols, which are conventional form-meaning pairings, as used in written numerals

300 and religious or political emblems in art. The meaning-specification role of semantics is
301 thought to occur predominantly within a symbolic system (Speaks, 2021) because the
302 ‘definite’ fixed pairing of a sense with a referent (Frege, 1948) appears to correspond to
303 conventionalised form-meaning pairings that characterise symbolic signs (e.g. Deacon,
304 1997). We purposefully avoid stating that symbols are *arbitrary* form-meaning pairings, as
305 proposed by Saussure (1966), because we will shortly address this point in the third
306 connection to semantics, the role of context, and because not everyone agrees with the
307 prominence of the arbitrary quality of symbols. Deuchar (1996), for instance, argues that
308 conventionality is more integral than arbitrariness, because not all language is arbitrary, and
309 because, although arbitrariness tends to happen naturally over time (Watson *et al.*, 2022),
310 conventionality is the crucial aspect for symbol creation and usage.

311 The semantic–symbolic connection is also supported by the proposed context-independent
312 nature of semantics and an alleged arbitrariness of symbols (Saussure, 1966), which is the
313 third more distinct use of the term *semantics*. Where communication is concerned, much of
314 the literature tends to separate out *semantics* from *pragmatics* (e.g. Devitt, 2021; Gutzmann,
315 2020). This distinction relates to the frequently held notion that semantic signals can be
316 thought of in terms of either a conventional meaning independent of any context (a situated
317 instance), or pragmatically in terms of the ways in which the signals exceed their
318 conventional meaning in a specific usage situation. This could include novel use or stretching
319 the scope of a word like ‘interesting’, which caters not only for describing genuinely
320 intriguing topics but also topics we politely have to suffer for a friend. This semantic–
321 pragmatic distinction also relates to the difference between *denotation* and *connotation* (Mill,
322 1882), where denotation is thought to concern core semantic meaning, in contrast to any
323 further associations, context, other attributes, and implications that enhance this meaning
324 (connotation). For example, one view holds that the meaning or content of a signal is

325 “information that has become ritualised and decoupled from the relevant contexts” and thus
326 semantics is borne of pragmatics (Skyrms & Barrett, 2019, p. 37). So, the signal/word ‘cat’
327 could refer conventionally to any cat, or ‘cat’ could refer to a specific cat in the vicinity,
328 whose identity is determined on the basis of pragmatic (or contextual) information.

329 This distinction between semantics and pragmatics also led to the creation of the term
330 *functional reference* (Macedonia & Evans, 1993; Berthet *et al.*, 2018). This term describes
331 how non-human signals are elicited by a specific class of stimuli that cause adaptive
332 behaviour notably in the absence of context, so that non-human communication may appear
333 to correspond to the referential quality of language(s) but only in a superficial way given the
334 uncertainty over the complexity of non-human communication and active intentionality.

335 Functional reference can be applied to chicken (*Gallus gallus domesticus*) food calls (e.g.
336 Evans & Evans, 1999), or in discussions of vervet monkey (*Chlorocebus pygerythrus*) alarm
337 calls, where each call seems to refer (or at least co-relate) to a specific predator (Seyfarth *et*
338 *al.*, 1980). However, the value of the term functional reference has been questioned (e.g.
339 Wheeler & Fischer, 2012). Moreover, there are challenges to keeping semantics apart from
340 pragmatics.

341 Semantics is usually deemed contextless, as with Hockett’s *semanticity* (Hockett, 1959;
342 Hockett & Altmann, 1968), one of a set of design features that Hockett argues separates
343 language from (animal) communication. From this perspective it is thought that “referential
344 signals should be sufficient, in the absence of the eliciting stimulus and of other normally
345 available cues, to allow receivers to select appropriate responses” (Macedonia & Evans,
346 1993, p. 180). Yet, there are those who argue context is always involved in meaning and
347 linguistic expressions of that meaning. For instance, reference does not necessitate
348 independence from context: a simple phrase like ‘the cat sat on the mat’ will relate to a
349 specific cat and a specific mat in a short story, on account of the use of the definite article

350 'the' rather than the indefinite article 'a' which pertains to the concept of 'cat', where no cat
351 is considered specifically. Therefore, definite contextual as well as indefinite contextless
352 reference exists. Yet, within the non-human literature, the context independence of semantic
353 relations is coalesced into a concept of referentiality for non-human communication, where
354 contextless reference is predominantly studied (e.g. Evans, 1997).

355 The relationship between a sense and its referent can be thought of as connecting semantics
356 and pragmatics because a referent is always situated within a context. Additionally, in
357 cognitive linguistics the *encyclopaedic view* of semantics (Evans, 2007) holds that no
358 meaning comes entirely context-free but instead concepts have a more stable core semantic
359 potential alongside a dynamic, ever-growing, structured inventory of associated knowledge
360 and contextual factors, which narrow down the scope of what may be 'meant' in the here and
361 now of the real world. This view is proposed, for instance, in Frame Semantics (Fillmore,
362 1976), in which meanings consist of an outline requiring details given by context. The view is
363 also proposed in the Theory of Domains (Langacker, 1987), in which all concepts are
364 connected to more global network structures in the mind. In these theoretical approaches, a
365 general concept or word's meaning incorporates specific world knowledge and does not
366 simply carry an inherently fixed contextless meaning.

367 To understand the important role of context, and thus pragmatics, consider a word like
368 'practice'. Its meaning is quite different when applied to a medical student who is learning
369 how to operate, as compared to the work of a professional surgeon, particularly from the view
370 of the patient. Moreover, as Beecher (2021) points out, a non-human signal like those of
371 vervet monkeys may be used to represent different things in different contexts, such as alarm
372 calls or intergroup fights, but the fixed sense and referent link remains within each separate
373 context, just as it does for human words that may be used polysemously (with more than one

374 meaning). For example, the English word ‘get’ can be used as relating to procuring an item or
375 understanding a concept, as in the phrases ‘I will get a drink’ or ‘I get what you’re saying’.

376

377 *(b) Pragmatics*

378 It is perhaps unsurprising that research has increasingly turned to the investigation of context-
379 based meaning or *pragmatics*. This applies not only for human-centric research including
380 some linguistic subdisciplines (e.g. Evans, 2015) but also the literature on non-human
381 communication (e.g. Seyfarth & Cheney, 2017). Scarantino & Clay (2015, p. e5) offer a
382 different definition than Macedonia & Evans’ (1993) definition of functional reference in
383 non-human communication. Scarantino & Clay’s (2015) definition highlights the role of
384 context because responses need to be contextually adaptive given the response cues that are
385 available. They give the example of vervet monkey alarm calls associated with leopards and
386 the monkeys’ responses of either running up a tree or standing bipedally when the monkeys
387 are on the ground at the time of the call, or running higher into a tree or looking about when
388 the monkeys are already in a tree.

389 Scott-Phillips (2015) goes further than others and argues that only pragmatic meaning may be
390 found amongst non-humans because conventionalised semantics evolved out of pragmatic
391 communication and non-humans have not reached the semantics stage. He states that non-
392 humans can determine relationships between the world, actions, and reactions in ‘coded
393 communication’, if not to the extent of ostensive-inferential communication as found in
394 language. Ostensive-inferential communication involves the expression and recognition of
395 communicative intentions (Grice, 1957; Sperber & Wilson, 1995) that are made possible by
396 *theory of mind* (Premack & Woodruff, 1978), which involves understanding the minds and
397 intentions of others. It is still debated whether theory of mind exists in non-humans [see
398 Krupenye & Call (2019) for a detailed review]. Scott-Phillips (2015) proposes that over the

399 course of human evolution conventional codes developed from this foundation of ostensive-
400 inferential communication. He argues that both pragmatics and analogies to the social-
401 cognitive mechanisms underpinning language should be sought in other species, rather than
402 semantic meanings.

403 This may be too rigid an approach, given some well-supported evidence of semantic-like
404 referential meaning demonstrated by a range of species within predator discrimination, food,
405 and social contexts [Table 1 in Townsend & Manser (2013), but see e.g. Clay, Smith &
406 Blumstein (2012) for counterarguments]. In any case, this evidence combined with Scott-
407 Phillips' (2015) arguments, the need to distinguish reference from semantics, and the
408 flourishing of pragmatic meaning study alongside semantics in linguistics, seriously
409 undermines arguments that non-humans are not capable of referential communication. This is
410 especially the case given that signals being context specific is no longer justification for
411 disallowing use of the term *reference*, functional or otherwise, for any species.

412 The tension between those who separate and those who argue for parallelism of semantics
413 and pragmatics is also important when we consider the study of pointing gestures. These
414 gestures clearly relate to some external entity, but lack a one-to-one semantic referential
415 mapping given the contextual basis of their use: one can point, and thus refer, to many
416 different things (Liebal & Oña, 2018). However, because of this, Byrne *et al.* (2017) argue
417 that this does not constitute a referential gesture, because it lacks strict semanticity. Rather,
418 this kind of gesture is deemed instead a deictic (fixed contextual) one, given the need for
419 additional information to be provided about what is being gestured towards and its location,
420 as with chimpanzee gestures. Yet, we advocate here that semanticity exists in parallel with
421 pragmatics and the requirement of context to stipulate the meaning in the real world. Again,
422 the occurrence of reference should not be limited to cases where there is a lack of context.

423 Scarantino & Clay (2015) recognised different uses for the term *context*, which should assist
424 with interpreting reference, including identity cues like age and social affiliation, gestures and
425 body orientation, environmental situation, and sequence combinations. Another nuance,
426 certainly for humans, amongst the complexity of context itself, is collocative context. Here
427 “You shall know a word by the company it keeps” (Firth, 1957, p. 11), i.e. the words or
428 phrases that commonly surround particular words can ascribe particular meaning to them. For
429 instance, speakers of English intuitively understand the differently nuanced meanings of
430 ‘catch’ in the phrase ‘catch the bus’ as opposed to ‘catch a ball’. Thus, context in the use of
431 communicative signals is complex and important for how meaning arises alongside
432 semanticity for both language(s) and non-human communication.

433 In summary, semantics is often used as a heading for its three associated phenomena:
434 reference, symbolic signs, and context (-independence). This can lead to confusion when
435 interpreting non-human communication. For example, chimpanzees engage in leaf clipping,
436 which is the repeated teeth ripping of leaves resulting in tiny blades that are not eaten but
437 discarded (e.g. Nishida, 1987). This activity may be used for gaining attention, even ‘flirting’,
438 or to demonstrate a feeling of frustration (Sievers & Gruber, 2020). This behaviour has been
439 proposed as an instance of non-human semantics or ‘arbitrary signals’ because the evolution
440 of leaf clipping cannot easily be explained, it appears conventional, and its multiple novel
441 functions are flexible and not fixed to a single context (Sievers & Gruber, 2020). Here,
442 *semantics* is used to relate to arbitrary and conventional signals, as well as context
443 independence. However, as discussed above, the nature of the sign/signal is not equivalent to
444 semantics, and must be considered separately. Meanwhile the context independence of
445 semantics is often paired with a pragmatic context in actual communication, so semantics
446 cannot be considered in total isolation of context. As such, whether leaf clipping may be seen

447 as semantic or not does not necessarily depend on whether it is an arbitrary signal or because
448 it is context independent.

449

450 **(3) Information transfer and influencing behaviour**

451 Another approach to studying meaning focuses on what meaning comprises: that is, what the
452 substance of meaning is and why we have (evolved) meaning in a communicative sense, i.e.
453 what does meaning achieve? This is also linked to reference, but is again not the same
454 phenomenon. Reference discusses the way in which meaning relates/is linked to imagined or
455 real entities and events, and mental representation: the ‘how of meaning’. The substance of
456 meaning discusses the types of *content* meaning has (Artiga, Birch & Martínez, 2020), or
457 *information* in other terminology (Shannon & Weaver, 1949). It explains the ‘what of
458 meaning’. For example, a signal/utterance may concentrate on experiencing the seasonal
459 weather or the anticipation of a holiday. It is often thought that the range of possible non-
460 human ‘topics of conversation’ is limited (e.g. Anderson, 2017). Yet, given that even the term
461 *meaning* has not yet been uniformly applied to non-human communication *per se*, perhaps it
462 is putting the cart before the horse to determine how limited or extensive the range of topics
463 of non-human meaning may be.

464 According to two seminal models of communication, information or meaning content was
465 thought to be either strictly carried within a signal along a communication channel (Shannon
466 & Weaver, 1949), or encoded and decoded within the minds of communicative interactants
467 (Saussure, 1966). In either case, the information or meaning content is intentionally signalled
468 by a signaller and actively inferred by a perceiver, with as much alignment and reduction of
469 uncertainty as possible, although some like Scott-Phillips (2010) question the value of such
470 code models. This is an extensive topic we return to in Section V.

471 Studies of non-human communication can also emphasise the behavioural aspect of the
472 communication, whether in terms of the function – the signaller’s immediate benefit from the
473 perceiver’s response, or in terms of the adaptive evolutionary benefit of the signaller, a
474 discussion we return to in Section VI. One clear instance of the behavioural focus of
475 communication is the study of the success of a signal’s influence on a perceiver’s behaviour
476 in a way that benefits the signaller (e.g. Owren, Rendall & Ryan, 2010). This is exhibited by
477 pale-winged trumpeters (*Psophia leucoptera*) giving a ‘mew’ contact call when they are
478 separated from others, which often elicits a loud ‘grunt’ call by conspecifics that is unique to
479 this context (Seddon, Alvarez & Tobias, 2002). This grunt facilitates the contact that the
480 original signaller sought to establish.

481 The notion of behavioural influence has developed in the evolutionary biology literature to
482 address two issues. Firstly, the likelihood of information transfer occurring within the
483 communication of other species has been questioned. Some propose that behavioural
484 influence is the main function of non-human communication rather than information transfer
485 because *information* is too vaguely defined, and because it excessively narrows the focus of
486 study (Rendall, Owren & Ryan, 2009). It has also been argued (Dawkins, 1986) that humans
487 cannot know what information a non-human perceiver has prior to any signal, and therefore
488 we cannot know the level of any reduced uncertainty. This makes the term *information*
489 unhelpful to explain non-human communication.

490 However, Dawkins’ (1986) point about not using the term *information* can be refuted because
491 whether the information is relevant or redundant for the perceiver does not necessarily affect
492 the informational content of a message or signal. For example, a newspaper whose headline
493 stories are already known to the reader still contains news, just old news as far as that reader
494 is concerned. Meanwhile, alarm calls may be repeated by an individual more than is
495 necessary to alert the group to impending danger, but this does not remove the alarm nature

496 of the call. Moreover, information comes in many forms as seen with longer alarm calls
497 potentially communicating a higher level of immediacy of danger to conspecifics
498 (McLachlan & Magrath, 2020), as well as information about a predator's approach. More
499 interestingly, acoustically similar calls can elicit different responses and *vice versa*;
500 meanwhile other animals can eavesdrop and pick up on the referent of a signal – perhaps
501 danger or a food resource – without the signaller's intent or awareness (Seyfarth *et al.*, 2010).
502 These instances demonstrate that at least some information exists within non-human signals
503 aside from any signaller manipulation. Additionally, Graham & Hobaiter (2023)
504 demonstrated that untrained humans appear to understand common non-human ape gestures.
505 This highlights evolutionary gestural connections and provides a window into the mind of
506 non-humans. So, while Dawkins (1986) may be right to be cautious in assuming human
507 observers can determine information transferred in non-human communication, this does not
508 mean that information transfer does not occur.

509 Additionally, given there is a need to explain how the signaller benefits from a
510 communicative interaction for it to have adaptive value, some have focused mainly on how
511 signals modify or manipulate the behaviour of recipients. Cues or accidental information
512 transfer exist. A predator can track prey by listening for their movement, for example in bats
513 that prey on katydids (Geipel *et al.*, 2020). Moreover, a range of species, including humans,
514 also frequently infer meaning without any active signalling. In Grice's (1957) natural
515 meaning category, clouds 'mean' or unintentionally indicate rain. However, this falls outside
516 of the evolutionary biology approach to communication because it focuses only on cue
517 assessment. From an evolutionary standpoint, all animals need to signal actively, and benefit
518 from these signals for the communication to persist, so some active influence on perceiver
519 behaviour is necessary to explain non-human communication.

520 Both information transfer and behavioural influence can actually be compatible achievements
521 of meaning in communicative interactions. For instance, information transfer can easily affect
522 perceiver's behaviour, as seen in the incontestable example of humans issuing a verbal threat
523 like, 'If you do not do your homework, you will lose television privileges', which would
524 usually lead to a child completing their homework, while a dog's growl will often cause a
525 stranger to feel threatened and back away. Moreover, the content of information can vary.
526 Signalling about one's affective or other physiological state or subsequent behaviour, like
527 smiling, can be as informative and still provide facts to the perceiver as much as signalling
528 about the external environment (Macedonia & Evans, 1993) like honeybees (*Apis mellifera*)
529 informing their hive companions about food sources (von Frisch, 1967). This corresponds to
530 transactional and interactive views of language in discourse analysis: how languages may be
531 used both informatively and interpersonally (Brown & Yule, 1983), often simultaneously, to
532 discuss everything from what the weather is on a given day, to how it feels to be waiting for
533 the bus in the rain and maintaining social bonds during the conversation. Further possible
534 functions of communicative interactions include aesthetics, as illustrated by poetry (Leech,
535 1974).

536 Information transfer and behavioural influence can also be seen as compatible when viewing
537 communication and its varied selection pressures in terms of both proximal-level information,
538 which helps perceivers to make decisions, and on the ultimate level, which explains why and
539 how perceivers behaviourally respond to signals (Font & Carazo, 2010). Additionally,
540 signaller and perceiver behaviours are thought to co-evolve (Bateson, 1966; Breed & Moore,
541 2016), so that the informational properties of signals are shaped as a consequence (Godfrey-
542 Smith, 2020). Scarantino (2013) therefore argues for a hybrid of the two in the study of non-
543 human communication. Otherwise, the problem is that either defining communication
544 exclusively in terms of only influence or in terms of information ignores either the main

545 driver of signal selection – influence, which has fitness benefits for signallers – or misses out
546 on the point that communication is distinguished from other types of influence, precisely
547 because signals benefit signallers *via* the information they transfer to perceivers.

548 The key distinction in the literature surrounding this meaning topic, therefore, ultimately
549 focuses on whether informational content is transferred actively by the signaller or is
550 perceived as a by-product of a behavioural display or by accident. This re-centres the
551 information transfer/behavioural influence debate on the existence and degree of
552 communicative intentionality within non-human communication and language, which would
553 support the ability to transfer information or influence behaviour actively.

554

555 **(4) Communicative intentionality**

556 Communicative intentionality can be linked to the act of making meaning when
557 communicating, where the active intentionality is key to both. Grice's (1957) famous
558 approach to conversational meaning is a seminal work within pragmatics, and is still
559 frequently cited (e.g. Terkourafi, 2021). It involves the active communication and recognition
560 of intentions, which leads to a successful transfer of meaning, whether this occurs as separate
561 to, or expressed by, language. Grice (1957) divides meaning into *natural* and *non-natural*
562 *meaning*. For example, when we see a cloud and consider that this 'means' rain, this is
563 tantamount to saying that the cloud indicates rain is about to fall. The cloud cannot intend to
564 cause rainfall any more than it can intend to mean, and so natural meaning concerns simple
565 correlations in the world. Thus, natural meaning pertains to the index sign type (Peirce,
566 1984).

567 Grice's (1957) non-natural meaning is more complex, usually relating to symbolic
568 communication in language, and, most importantly, involves intentionality and recognition of
569 that intentionality. Grice focuses on the role of overt intentionality, also known as ostensive

570 inference, which requires mental belief ascription to others (Bar-On & Moore, 2017) and the
571 active influence of others to take note of one's intended meaning. Consequently, this theory
572 proposes that for communicative meaning to arise, a signaller must have a goal and intend to
573 communicate that goal, like feeling thirsty and wanting to let a server at a cafe know this so
574 that one's cup may be refilled. Meanwhile the perceiver – here the server – needs to
575 recognise the goal as well as the signaller's intent to communicate that goal, so that they see
576 the lifted empty cup and recognise that the signaller is trying to get attention to notice the
577 empty cup, for it to be refilled.

578 Communicative intentionality has been widely discussed across disciplines. Both Halliday
579 (1975) and Tomasello (2003), for instance, argue that one of the fundamental aspects of
580 language is communicative intention. Furthermore, one of the key ontogenetic developments
581 of children's language acquisition is the fundamental act of learning how to mean, as per the
582 title of linguist Halliday's (1975) text, and learning that others intend to mean, alongside the
583 content of any particular meanings within their communication. Zlatev *et al.* (2018) also
584 highlight the dynamic nature of meaning, the 'meaning-making' aspect, which could be said
585 to form part of communicative intentionality too. Given the strongly central role that meaning
586 has within language, as asserted by many cognitive linguists (e.g. Dąbrowska, 2016; Evans,
587 2015; Lakoff, 1987), the two phenomena are tied together. It is perhaps no surprise then that
588 when non-human communication is compared to language, one of the key discussion points
589 is also to what degree other animals are capable of and engage in meaning-making, or
590 communicative intentionality.

591 Some argue that communicative intentionality is very simply a human-only capacity (e.g.
592 Tomasello, 2003), while Rendall *et al.* (2009) argue that non-human signallers fail to account
593 for perceivers' informational needs and so fail to demonstrate perspective taking and theory
594 of mind that can be considered fundamental to language. Others downplay meaning's need

595 for complex cognition including communicative intentionality, proposing intermediary levels
596 that may be found amongst non-humans, as well as pre-verbal infants. For instance, Moore
597 (2018) argues that using eye contact or similar gestures to attract attention to one's signal is
598 frequent and deliberate across species but does not require any reflection, the attributing of
599 communicative intent to a signaller, or inferring mental states to still fulfil the requirements
600 for Gricean non-natural meaning.

601 Alternatively, while great ape gestural communication may be deemed intentional, it can be
602 regarded as individualistic rather than cooperative (Tomasello & Call, 2019) because it fulfils
603 individualistic goals and not joint goals like humans: one can hunt with others for one's own
604 food more easily, or hunt with others to ensure everyone in the group obtains food, for
605 instance. Thus, it might be argued that this particular communication would not fulfil the
606 criteria for *joint attentional frames* (Tomasello, 2003), which are triadic situations of active
607 shared attention between two individuals with a third object or event that together create a
608 shared common ground for the communicative interactants. These joint attentional frames
609 allow for an understanding of communicative intentions and engagement in role-reversal
610 imitation to acquire and use symbolic conventions, all arguably needed for language
611 development. Others similarly propose that a more effective explanation of non-human
612 communication, and any meaning arising therein, is that non-humans engage in goal-directed
613 communication rather than intentional communication (e.g. Townsend *et al.*, 2017;
614 Zuberbühler, 2018). In other words, "signallers communicate, but they do not communicate
615 that they communicate" (Fischer & Price, 2017, p. 29).

616 Meanwhile others argue that certainly intentionality, if not communicative intentionality, is
617 fully present within non-humans, from Veit's (2022) discussion of ways to proceed with
618 comparative study of consciousness to the Cambridge Declaration on Consciousness (2012:
619 <https://fcmconference.org/>) stating that "Convergent evidence indicates that non-human

620 animals have the neuroanatomical, neurochemical, and neurophysiological substrates of
621 conscious states along with the capacity to exhibit intentional behaviors”. In fact, and most
622 importantly for this discussion, one statement made elsewhere about bonobos (*Pan paniscus*)
623 is that “Because the gestures are intentionally produced, these outcomes are not only the
624 gestures’ ‘functions’—they are their ‘meanings’” (Graham *et al.*, 2018, p. 9; also Byrne *et al.*,
625 2017).

626 Therefore, while debate continues about the degrees to which other animals exhibit
627 communicative intentionality, the phenomenon is clearly linked to discussions about meaning
628 and therefore forms part of any theoretical framework describing meaning – and non-human
629 communication must be part of this discussion. Moreover, just as Grice’s (1957) focus on
630 overt intentionality also relates to the notion of influencing others’ behaviour, as with our
631 previous discussion on information or behavioural influence as the main driver for
632 communication, there are clearly multiple considerations required to understand meaning.

633

634 **(5) Multifaceted theories of meaning**

635 Another noticeable trend in the literature, although the importance of this has not been made
636 explicit until now, is that meaning is multifaceted. As mentioned above, Grice (1957) breaks
637 down meaning into two forms: natural and non-natural meaning, where only the latter is
638 deemed important for communication between conscious interactants and can be considered
639 true meaning. However, according to Kalantzis & Cope (2020), five functions can be found
640 in any meaning: reference, agency, structure, context, and interest (expressing purpose).

641 Leech (1974) classifies meaning into seven ‘ingredients’ with primary importance placed on
642 ‘conceptual meaning’, which relates to semantics and denotation. Leech’s (1974)
643 ‘connotative meaning’ includes what conceptual meaning refers to, as with Frege’s (1948)
644 referents (contrasting with sense). Leech (1974) adds types of associative meaning: ‘stylistic

645 meaning' for social use; 'affective meaning' relating to emotions; 'reflected meaning'
646 relating to semantic networks that are conjured mentally when one concept arises; and
647 'collocative meaning' in terms of linguistic environmental associations. Lastly, Leech (1974)
648 proposes 'thematic meaning,' which involves organisation by a signaller in terms of ordering,
649 focus, and emphasis. To Leech (1974), meaning in a wider sense can be termed
650 'communicative value'. Ogden & Richards (1946, pp. 186–187) compiled a list of over 20
651 definitions of meaning. These include meaning being described as an intrinsic property, a
652 connotation of a word, an essence, a volition or intended event, practical or theoretical
653 consequences of events or utterances, and that which a user or an interpreter refers to. In sum,
654 the literature pertaining to humans at least, where meaning is not only generally accepted but
655 is also analysed extensively across disciplines, demonstrates that meaning is a complex
656 phenomenon, and it appears to have multiple facets. What is of particular interest is that when
657 the literature across disciplines and species is compared, similar themes emerge that facilitate
658 the development of a comparative framework like the one we develop here.

659 Speech act theory (Austin, 1975) is a particularly useful basis upon which to discuss the
660 topics and arguments relating to meaning that emerge across disciplines and species. As a
661 philosopher of language, Austin's (1975) work is relevant because it presents a tripartite
662 breakdown of how human utterances operate and how they contribute meaning to a
663 conversation. This is a seminal work, still relevant in research today (e.g. House & Kádár,
664 2021; Schmid, 2020), including work on emotional expressions operating as appeals to
665 recipients for calls to action using Austin's distinctions (Scarantino, 2017).

666 Austin's *locutionary speech acts* refer to utterances *per se*: the surface meaning of the words
667 in the statement or question that involve the sense and referent. So, if you asked someone at
668 dinner 'Is there any salt?' it might be interpreted as if you were wondering about the
669 existence of salt in the world (serving as a possible referent for the word *salt* in this question).

670 *Illocutionary speech acts* refer to the hidden meaning, implication, or layered meanings that
671 co-exist with the surface meaning of the utterance. In this instance, when you ask ‘Is there
672 any salt?’ a more likely interpretation is that you are asking about the existence of salt in the
673 vicinity of the meal, or one step further, that you are enquiring about the salt’s close
674 proximity because you wish to obtain some to add to your meal to enhance its flavour.
675 However, none of that information is actually expressed in the utterance itself. The third
676 *perlocutionary speech acts* relate to the outcome of an interaction. Therefore, once you have
677 asked ‘Is there any salt?’ and your dinner companion has inferred that you are implying the
678 question ‘Is it possible (and acceptable) for me to acquire some salt to put onto my dinner?’
679 your companion may respond in any number of ways. This might include pointing to where
680 the salt is kept, ignoring your question altogether, or cooperatively fetching the salt and
681 placing it next to your plate. An interpretation of non-human communication based on speech
682 act theory could be a growl from a dog in a play context. The surface meaning of the growl is
683 an aggressive threat display to warn another animal to stay away. However, the hidden
684 meaning, that the growl is only an empty gesture, may be revealed by the dog’s concurrent
685 provision of a toy, which will encourage perceivers to interpret the growl as a play signal
686 instead of an aggressive signal. As a result, the perceiver may be encouraged to engage in
687 playful activity with the dog.

688 Therefore, Austin’s (1975) speech act theory describes how there are different aspects of
689 meaning contained in and around an utterance, or *communicative signal* in more
690 interdisciplinary terminology. However, rather than simply cataloguing different types of
691 meaning, like Ogden & Richards (1946), Austin’s (1975) framework presents three clearly
692 defined and distinct functions of communicative signals and ways in which meaning arises.
693 Importantly, meaning does not just have to be carried or encoded by the signal itself, as
694 assumed in traditional semantics or information theory (Shannon & Weaver, 1949), or as

695 Saussure (1966) describes, where meaning is packaged and unpackaged as similarly as
696 possible in the minds of the signaller and perceiver. Rather, as per the term coined by Grice
697 (1975), there can also be *implicature* involved: that is meaning that is not strictly signalled
698 but is hinted at, suggested, and implied. Moreover, it may be argued that meaning is not fully
699 realised until an understanding is achieved on the part of the perceiver, and an outcome of a
700 communicative interaction occurs that coheres in some way with the original signal and/or
701 implicatures, to the benefit of the signaller for adaptive fitness. Austin's (1975) work thus
702 raises the important question of where the meaning arises within a communicative
703 interaction, if it is not a blend of all three aspects: the signal, the intentions and context
704 behind and around the signal, and the outcome(s) of the signal. This also relates to Ongstad's
705 (2021) breakdown of communication into a triad of form, reference, and act.

706 Essentially, there are very different approaches and foci across disciplines when it comes to
707 the subject of meaning. Overall, one way to differentiate the main variation lies in thinking of
708 meaning either in terms of abstract relations or reference, or in terms of social influence.

709 Within human-centric research, mental representation and the nature of concepts, overt and
710 covert intentions, as well as how these are expressed symbolically form the focus of study,
711 especially given the confidence of such attributes in human cognition. From an evolutionary
712 perspective, the focus remains closely tied to the functional role of meaning, including
713 behavioural influence and the fitness benefits acquired from communication, which has led to
714 discussions of information transfer *versus* behavioural manipulation as the main purpose of
715 communication. This is not tantamount to suggesting that meaning is a different phenomenon
716 depending upon discipline or indeed species. Rather, the apparent distinctions may come
717 down simply to the fact that we struggle to measure mental representation and abstract
718 relations in non-humans, and this limits our focus to their behaviour.

719 Having broadly explored the key themes and terminology relating to meaning across
720 disciplines and species, it is clear that there is complexity, nuance, and variation in how
721 meaning is discussed. More importantly, it becomes clear that meaning has multiple facets to
722 it and that it is (at least partly) contextually dependent. Austin's (1975) tripartite analysis of
723 speech acts, as detailed above, aligns most closely to the various discussions of meaning
724 across disciplines and species, although this was never the original intent of Austin's work.
725 One overall point, which particularly stands out, is that most of the literature does not
726 actually question or attempt to define the concept of meaning itself. Instead, different fields
727 have focused on different facets of meaning: from how and where it is encoded, to the
728 signaller and perceiver's possible roles in how meaning arises, to what possible outcomes
729 derive from communicative interactions, and how they align with the goals of the signaller
730 and/or perceiver. In short, we are discussing one phenomenon with different facets. There are
731 not many different types or definitions of meaning, but rather there are numerous
732 'ingredients' of meaning to use Leech's (1974) term.

733

734 **III. A MULTIFACETED MEANING FRAMEWORK**

735 **(1) A multifaceted framework**

736 Given the cross-disciplinary review in Section II, there seems to be strong agreement across
737 disciplines that whatever meaning is, it is an important aspect of communication (e.g. Austin,
738 1975; Grice, 1975; Higham & Hebets, 2013). It involves conceptual representation, as well as
739 expression in a communicative setting (e.g. Evans, 2016; Fitch, 2019). It involves some
740 degree of goal-directedness, if not full (communicative) intentionality (e.g. Grice, 1957;
741 Halliday, 1975; Moore, 2018). It requires a response on the part of the perceiver (e.g. Rendall
742 *et al.*, 2009; Ruxton & Schaefer, 2011). Additionally, the outcomes of a communicative
743 interaction must be consistent with the signaller's goals and/or intentions, often referred to as

744 functional or fitness benefits in the non-human literature (e.g. Artiga *et al.*, 2020; Grice,
745 1957; Ongstad, 2021). Different disciplines concentrate on different aspects or facets of
746 meaning largely through tradition or necessity, while meaning itself is multifaceted but still
747 represent one phenomenon that arises within communication.

748 This point – that meaning is multifaceted – motivates our creation of a unified theoretical
749 framework to be used across disciplines and species. Such a framework begins with accepting
750 meaning as an umbrella term. Understanding it as a multifaceted but still unified concept
751 allows us to attribute the term *meaning* to non-human communication whenever we discuss
752 part of meaning in relation to other species, from reference to active signalling to the
753 functional value and outcome of signals.

754 As such, we posit three fundamental meaning facets that are essential to create a coherent and
755 comprehensive theoretical framework. These facets loosely correspond to Austin's (1975)
756 locutionary, illocutionary, and perlocutionary acts, modified to permit interspecific
757 comparison. These meaning facets can intersect and coexist in a single communicative action.
758 The evolutionary relationships between these meaning facets are consistent with discussions
759 of semantics and pragmatics in human-centric literature and can also be studied at all levels
760 proposed by Tinbergen (1963).

761 As Table 1 illustrates, Austin's (1975) framework is a productive way to integrate discussions
762 about meaning in communication for both humans and non-humans because it includes
763 surface meaning, implied meaning, and meaning outcomes. This provides a useful basis for
764 the three meaning facets we will describe, alongside their related topics and discussions, such
765 as reference, intentionality, and fitness benefits. In fact, all three meaning facets, associated
766 with signals, interactants, and action outcomes, occur in just one sentence in an article on
767 non-human behaviour: “the calls and gestures the animals produce, the attention they show to
768 one another, the extent to which one animal's actions ‘fit’ with another's, etc. - are all

769 familiar aspects of what we typically think of as animal communication” (Johnson, 2015, p.
770 231 [emphasis added]). The rest of this section describes how Austin’s (1975) theory
771 motivates and creates a foundation for our theoretical framework of meaning. Following this,
772 we discuss each of the three proposed meaning facets in more detail.

773

774 **(2) Austin’s speech acts as a basis to understand meaning**

775 Austin’s (1975) locutionary speech acts and related topics focus on the meaning of the signal
776 itself, without any further consideration of signaller intent or how the perceiver might
777 respond. This aligns with the proximal mechanisms level of Tinbergen’s (1963) principles for
778 studying animal behaviour, as well as what affective or other informative content may be
779 involved in a signal. The locutionary act may involve peripheral discussions too, like models
780 of communication, including Shannon & Weaver’s (1949) flow of information system. This
781 notion of transmission of information links to discussion of contextless meaning-carrying
782 semanticity of signals. Evolutionary biologists also consider the nature of the locutionary
783 speech act as being subject to constraints driven by the trade-off between information content
784 and cognitive simplicity (Ferrer-i-Cancho & Solé, 2003; Kershenbaum *et al.*, 2021).

785 Austin’s (1975) illocutionary acts neatly pair discussions of implied meaning or connotation,
786 perceiver inference, and overt signaller intentionality as discussed in human-centric studies,
787 with the question of intentionality in other animals. While mental representation and concepts
788 are no longer widely disputed among non-humans (Fitch, 2019), communicative
789 intentionality is still questioned (e.g. Tomasello, 2003). This second aspect aligns with
790 Tinbergen’s (1963) function (more immediate survival value) level of studying animal
791 behaviour.

792 In both speech act comparisons, non-human communication and any meaning it may involve
793 have been studied in how they relate to language. However, non-human communication and

794 any potential associated meaning are studied in behavioural terms too. This is captured best
795 in relation to Austin's (1975) perlocutionary speech acts, or outcomes of a communicative
796 interaction, as well as two of Tinbergen's (1963) principles for studying animal behaviour:
797 ontogeny and evolutionary history, given the proximal response and benefit(s), or *function(s)*,
798 as well as longer-term adaptive value(s) of successful communication. This situates the
799 current debate about the purpose of non-human communication: is it used for information
800 transfer or to manipulate perceiver behaviour?

801 There are other related but more peripheral aspects to these three central notions. Where
802 locutionary acts, and more specifically semantic meaning or denotation, are concerned, this
803 can spark the discussion of what form the signal may take. This includes an arbitrary or
804 conventional form-meaning pairing as with symbols, indexes as in Grice's (1957) natural
805 meaning, or perhaps involves paralinguistics, communicative features that are not categorised
806 as linguistic but carry communicative meaning, from intonation to a well-timed cough. Given
807 that these discussions centralise the form and operation of the signal itself, and any meaning
808 therein, a more peripheral discussion is how exactly the meaning becomes encoded within the
809 signal. For instance, is compositionality involved? Is meaning encoded in a multimodal way?
810 Or does structural complexity carry the meaning? Are the signals graded or discrete? Is
811 meaning a reification (a thing), or part of a dynamic cognitive process of the signaller and/or
812 perceiver? Is there a blend thereof?

813 Within discussions relating to illocutionary acts, we can of course question the role of
814 intentionality, inference, and theory of mind within meaning, including to what degree other
815 species are capable of these cognitive processes. Additionally, we can also situate discussions
816 about honest signalling and deceptive intent. Furthermore, this situates discussions about the
817 role of context and pragmatics.

818

819 (3) Three facets of meaning

820 Now that we have explored the interrelated concepts and considerations for understanding
821 meaning, including its multifaceted nature, and demonstrated that Austin's breakdown of
822 speech acts neatly correlates to these issues, we will describe the global meaning facets.
823 There are three key facets of meaning (Fig. 1): (a) meaning pertaining to the signal, the
824 *Signal Meaning Facet*; (b) meaning pertaining to the communicative interactants, as well as
825 context, the *Interactant Meaning Facet*, with subdivisions focusing on the signaller or the
826 perceiver; and (c) meaning pertaining to the outcome(s) of communicative interactions or
827 *Resultant Meaning Facet*, whether this outcome relates to immediate fitness or a longer-term
828 evolutionary benefit, with a small subdivision for where the perceiver also benefits. These
829 terms have been created to avoid conflation with other relevant but much more niche,
830 contextual and/or discipline-specific terms, like *function*, *sign*, or *semantics*, which currently
831 complicate matters when attempting to bridge disciplines and species. We will describe in the
832 following sections how our three suggested meaning facets relate to the literature in both
833 human and non-human communication, verbal and non-verbal. The mental processes used in
834 Fig. 1 are for ease of illustration and an accessible way into the concepts, as we note that we
835 do not have full familiarity with non-human minds as yet.

836 To substantiate our own framework further, a recent paper (Watson *et al.*, 2022) has created a
837 framework for studying part of the evolution of arbitrariness in (non-)human communication
838 that mirrors the same type of approach we take herein for the study of meaning. Watson *et al.*
839 (2022) propose five dimensions in their framework involving: signal production, signal
840 adjustment, signal usage, combinatoriality, and signal perception, which partially correlate to
841 our three key facets outlined above. However, Watson *et al.* (2022) avoid discussion of
842 meaning, whereas we focus on this very topic, due to the difficulty of defining meaning and
843 the contentious debate over whether non-human signals involve meaning. Watson *et al.*

844 (2022) opt for more ambivalent ‘communicative function’ terminology. Similarly, Raviv,
845 Peckre & Boeckx’s (2022) explanation of the apparently inverse relationship between social
846 complexity and signal variability exhibited across humans and non-humans works on the
847 basis that meaning cannot be inferred for other animals’ communication. The authors note
848 that we can only distinguish non-human signal variability based upon the signal’s distinctive
849 features, akin to the approach taken to linguistic phoneme (sound form) analysis before the
850 layer of meaning is built in for human communication. At this purely phonemic level, the
851 variability increase, for bigger and more complex societies, is fairly consistent across species.
852 However, when pairing phonemes with their referent, giving the sound signal a layer of
853 meaning, this reduces the levels of possible variability within human communication and
854 establishes more conventionality or arbitrariness. Thus, establishing meaning in non-human
855 communication would lead to a vastly different interpretation of the evidence put forward by
856 Raviv *et al.* (2022).

857

858 **IV. SIGNAL MEANING FACET**

859 Having established the three global meaning facets, we now consider each one in more detail
860 and illustrate them using with relevant cross-species discussion and examples. The first facet
861 of meaning, the Signal Meaning Facet (b in Fig. 1), pertains to the way in which meaning is
862 conveyed, and involves both the content of the signal and how meaning is encoded within the
863 signal. The Signal Meaning Facet loosely relates to Austin’s (1975) locutionary speech acts
864 and includes a focus on the apparent meaning of the signal, often couched in terms of
865 *semantics*, where arbitrary convention and contextless meaning are discussed. The Signal
866 Meaning Facet and its associated discussions have received the most attention in the literature
867 across disciplines.

868

869 **(1) The signal and its content**

870 Even the notion of what a signal is has attracted considerable attention. Scott-Phillips *et al.*

871 (2012) state that *communication* involves both a signal and a response behaviour, which are

872 functionally interdependent. Meanwhile, Maynard Smith & Harper (2003) and Higham &

873 Heberts (2013) note that *signals* are traits that have been selected for their communicative

874 function, whereas *cues* have not and are incidental.

875 One important aspect of the Signal Meaning Facet is the actual content or information of any

876 signal meaning. Semantics as a mode of meaning is thought to involve core concepts: truth,

877 aboutness (related both to reference and intentionality), and topic (subject matter), but only

878 the first two have been treated extensively within human-centric studies (Hawke, 2018). Still,

879 the topic or content of meaning is integral where communication is concerned. It has been

880 clarified that information does not simply relate to objective facts external to the signaller but

881 can also include reference to the signaller's affective (emotional) state or their intentions. One

882 example would be a deceptive communication that contains information that is strictly false

883 but faithfully reflects the signaller's intention. However, what topics may be covered within

884 non-human communication remain somewhat elusive and underexplored, particularly while

885 scholars continue to question the bigger issues, including whether non-humans are capable of

886 meaning at all. We hope this framework will help to end this debate by showing that at least

887 some non-humans are not only capable of meaning but that the facets of meaning can be

888 demonstrated in their communication. Understanding the full extent of meaning in non-

889 human communication is then limited only by methodological constraints, and the level and

890 breadth of data gathered.

891 Another aspect to consider in terms of a signal's content is the *granularity* or "cognitive

892 zoom" (Tenbrink, 2020, p. 118; Mann & Hoeschele, 2020) at which the signal provides

893 content. Often non-human signals are categorised quite coarsely, for instance mating calls

894 *versus* food calls or other ‘prosaic’ categories (Byrne *et al.*, 2017). However, whether this
895 adequately reflects the actual level of detail of content within the signal remains to be seen.
896 Even with humans we can categorise our communication very generically, such as complaint
897 or compliment, or go into depth about the specific nature of what has been discussed, from a
898 compliment generally to a more detailed commendation of a colleague’s hard work on a
899 particular project.

900

901 **(2) Shannon and Weaver model of communication**

902 Where and how is the meaning associated with the signal? How is it encoded in the
903 communicative interaction? This is another major part of the Signal Meaning Facet. One
904 common way to answer this question is a recourse to models of communication, notably
905 Saussure’s speech circuit model (Daylight, 2017; Saussure, 1966) and the Shannon & Weaver
906 (1949) model, both of which view communication as a transmission, with information
907 encoded and decoded by the signallers and perceivers, which should correlate as closely as
908 possible and so reduce uncertainty in the perceiver. The enduring Shannon & Weaver model
909 of communication breaks down the human communicative process into five parts:
910 information source, transmitter, the channel to transmit the signal, a receiver, and the
911 destination or person for whom the ‘message is intended’ (Shannon & Weaver, 1949, p. 34),
912 like sending a telegraph. This perspective is embedded in language also (certainly English),
913 as shown by Reddy’s (1979) Conduit Metaphor, with examples including ‘Try to get your
914 thoughts across better’, in which the thoughts are described as being channelled from one
915 mind to another, almost like water flowing through a conduit. However, where Shannon &
916 Weaver (1949) focus on the transmission itself, Saussure (1966) focuses more on the
917 communicative interactants and claims that meaning arises only in their minds, with any
918 transmission being nothing more than sound waves. Yet, there are numerous other ways in

919 which a message/content/meaning can be conveyed or can arise in a communicative
920 interaction. This is the reason we have adopted the term *perceiver* instead of *receiver*
921 alongside *signaller*.

922 For instance, Peirce (1984) noted that there is a triadic set of forms that a sign or signal may
923 take. To reiterate, it is important to note that these forms, and especially symbols (arbitrary
924 form–meaning pairings; Saussure, 1966), are not the same as reference (Liebal & Oña, 2018;
925 Pepperberg, 2017), although they can be used referentially to communicate about the world.
926 Within language, symbolic reference is commonly found but should not be discussed to the
927 exclusion of other sign types. For example, there is a growing body of work on iconicity
928 within linguistics that explores topics like the onomatopoeia in ‘crack’ and how words can
929 sound very similar to the actual entity they represent (e.g. Perniss, Thompson & Vigliocco,
930 2010). Therefore, all sign types should be explored within non-human communication too.

931

932 **(3) Multimodality**

933 Another aspect of language and communication which should not be ignored for its potential
934 to yield meaning within a signal is multimodality, so the Signal Meaning Facet needs to
935 involve this. Shannon & Weaver (1949) proposed a unimodal transmission by signallers, with
936 meaning encoded in the signal, given their model was based upon telecommunications.
937 Moreover, the vocal–auditory channel continues to be the main modality explored in non-
938 human communication research (e.g. Fishbein *et al.*, 2019). However, meaning does not need
939 to emerge from a single modality, and there is a rich literature on multimodal communication
940 (e.g. Higham & Hebets, 2013). Various modalities offer different transmission distances and
941 levels of permanence, and are detected in diverse ways by species, allowing for close-range
942 private or broadcast communication. Meanwhile, different modalities can also contribute
943 different parts of an overall message from a signaller, such as paralinguistics adding to

944 speech, including one's tone of voice or hand gestures. Another instance would be the
945 courtship display of male wolf spiders (family Lycosidae) (Stafstrom & Hebets, 2013), which
946 wave their ornamented forelegs with an accompanying seismic signal. These multimodal
947 displays yield higher mating frequencies than producing the signals separately, suggesting a
948 proximal meaning is attached to the multimodality.

949 Given that meaning can occur in any of the separate modalities or blend thereof (see also
950 Pleyer, Lepic & Hartmann, 2022), this highlights that meaning can arise within structural
951 complexity, as it does with syntax in the case of language. Many argue for compositional
952 semantics, which involves the meaning of an expression being built up from both the
953 meaning of its individual parts and from how each expression is combined syntactically. One
954 kind of syntactic arrangement, hierarchical as opposed to linear syntax, is deemed unique to
955 humans (e.g. Bolhuis *et al.*, 2018). This allows for embedding additional meanings within a
956 sentence, as with 'The malt that the rat that the cat killed ate lay in the house that Jack built.'
957 This formalist compositional approach to meaning structure is what Suzuki *et al.* (2020) term
958 a *syntax–semantics interface* and there is limited evidence that such complex messages are
959 encoded by non-humans (Engesser & Townsend, 2019; Schlenker, Chemla & Zuberbühler,
960 2016).

961

962 **(4) Gestalt principle**

963 An alternative view to the formalist compositional approach to meaning structure holds that
964 not everything can simply be the sum of its parts, as with idioms like 'kicked the bucket'
965 which is used to refer to someone dying rather than literally kicking a bucket. This approach
966 is known as the gestalt principle, part of a movement in psychology (Evans, 2007; Lakoff,
967 1987), and it applies as much to grammar as to the lexicon (vocabulary), like
968 compositionality. The gestalt principle can be seen in the various Construction Grammar

969 theories that have been proposed (e.g. Goldberg, 2019), which propose that learned form–
970 meaning pairings are the building blocks of language, and also by Blending Theory
971 (Fauconnier & Turner, 1996), in which not only new meanings but also new linguistic
972 structures can emerge from the combination of linguistic units that are above and beyond a
973 simple addition of individual parts. This yields amusing compound nouns like ‘bookworm’
974 and unusual phrases like ‘I sneezed the napkin off the table’, where a more traditional
975 grammatical sentence might phrase this as ‘I sneezed and the napkin blew off the table.’
976 Arnold & Zuberbühler (2012) touch on gestalt when discussing an alarm call sequence used
977 by putty-nosed monkeys (*Cercopithecus nictitans*) that the researchers refer to as ‘idiomatic
978 expressions’. Of the calls that these monkeys produce, their ‘pyow–hack’ sequences
979 concatenate their separate ‘pyow’ or ‘hack’ calls which convey a different meaning entirely.
980 The ‘pyow’ and ‘hack’ and various ‘hack–pyow’ sequences refer to external events, such as
981 specific predator types, and elicit responses including vigilance. Yet, short ‘pyow–hack’
982 sequences elicit the group’s travel, and the researchers liken this to human idiomatic
983 expressions like ‘kick the bucket’, where the meaning is not simply derived from its parts.
984 However, this is not the “syntactic dead end” (Arnold & Zuberbühler, 2012, p. 308) that the
985 researchers suggest. Instead, the gestalt principle supports the idea that ‘pyow–hack’
986 sequences are an example of a very language-like instance of animal communication.
987 Moreover, the researchers point out that ‘idiomatic expressions’ enable signallers to increase
988 the number of messages that can be conveyed by the small repertoire.
989 Another intriguing example where the gestalt principle might occur within non-human
990 communication is seen in dwarf mongoose (*Helogale parvula*) alarm calls (Collier *et al.*,
991 2020). This species produces at least three meaningful alarm calls: one for aerial predators,
992 one for terrestrial threats, and a T₃ call which seems to comprise the two other alarm calls that
993 functions as a general alarm to threats. The researchers explore the interpretation of the call’s

994 structural analysis, but a gestalt interpretation may be adopted here. The researchers describe
995 the T₃ call as “a stand-alone, holistically meaningful call” (Collier *et al.*, 2020, p. 6), which,
996 provided the unit order remains the same in every T₃ call, seems similar to a human idiom,
997 and this interpretation therefore fits the gestalt principle. This is supported because the two
998 subunits of the call are actually two separate mongoose alarm calls: one for aerial predators,
999 the other for terrestrial predators. The meaning of the T₃ call appears, however, to be a
1000 general threat, because of the behaviour of the mongooses: the “absence of differences in
1001 reaction strength to T₃ and aerial or terrestrial calls” (Collier *et al.*, 2020, p. 4). Thus, the call
1002 might act as a category label referring to threats in general, including ones that are not so
1003 easily distinguished into terrestrial or aerial predators, perhaps in the way that we might shout
1004 ‘Danger!’ as opposed to the more specific ‘Fire!’ or ‘Gun!’

1005

1006 **(5) Discrete and graded signals**

1007 A further point to address when considering ways in which meaning is associated with a
1008 signal is the discrete and graded nature of signals: whether signals are distinct or continuous,
1009 like alarm calls that differentiate between predator types as opposed to signals relating to
1010 more graded emotional expressions (Larter, 2022). In non-humans, graded signals are alleged
1011 to be most common (e.g. Studdert-Kennedy, 2005), and discrete signals are thought to be rare
1012 potential indicators of referential meaning. However, is this rarity because there is a
1013 difference in how we (are able to) transcribe non-human communication and languages, and
1014 the lack of a non-human International Phonetic Alphabet equivalent? Or is this based on
1015 whether the communication can be categorised as meaningfully discrete for the species using
1016 the communication (Kershenbaum *et al.*, 2016), like the compositional account of semantics
1017 outlined above? In any case, compositionality is not the sole way in which meaning can be
1018 constructed. Although language is typically associated with discrete signals encoding specific

1019 meaning, graded forms and flexible meaning patterns do exist (Taylor, 1995, 2019). For
1020 instance, grammaticalisation is frequent, in which words change their syntactic function
1021 (sentence use) over time (e.g. Croft, 2003). So, the English phrase ‘going to’ was once
1022 restricted to referring to actual motion towards a target location, e.g. ‘I am going to Dublin’,
1023 but has evolved to also refer to intended future actions, as in the statement ‘I am going to
1024 finish reading this article’. All linguistic categories need to be continuous to a degree, due to
1025 the gradually occurring diachronic changes to language (Bybee, 2007). The song of male
1026 humpback whales (*Megaptera novaeangliae*) changes over time too, mostly with small
1027 transitions, as it spreads across populations from west to east (Garland *et al.*, 2011), which
1028 might involve a non-human parallel with grammaticalisation, or at least diachronic sound
1029 change, which could have meaning implications. Meanwhile, modal expressions like ‘should’
1030 have graded meaning (Lassiter, 2020), from a weak suggestion from a friend ‘You should try
1031 reading this book’ to a much stronger statement on a UK government website relating to
1032 travel rules during the Covid-19 pandemic ‘This vaccination proof should be provided.’

1033

1034 **(6) Dynamic signalling**

1035 A final factor to consider in terms of meaning encoding for the Signal Meaning Facet is
1036 whether we conceptualise meaning as a reification (an almost tangible entity), or as a
1037 dynamic cognitive process. Is meaning a static phenomenon that we simply need to find the
1038 criteria for and can then compare communication systems against to determine if they do
1039 incorporate meaning? Or is meaning an online construction (built by the brain in the
1040 moment), for instance as a result of interactant cognition and in relation to changing
1041 situations? One reason for this consideration is Croft’s (2011) discussion of language as a
1042 process rather than a static phenomenon, given its general cognitive basis and that the nature
1043 of cognition is inherently dynamic. Due to the close relationship between language and

1044 meaning, such an approach may be adopted by analogy to meaning. Croft's argument is used
1045 here in addition to Skyrms' (2010) point that signalling structures are not closed fixed
1046 interactions but are open and adaptable across species, and they involve a process of
1047 cooperative coordination between signallers and perceivers. This is in addition to the many
1048 other aspects that are involved in meaning-making, from mental representation to the role of
1049 the communicative interactants themselves.

1050 Whatever the ultimate and comprehensive nature of meaning in all its finer detail, the Signal
1051 Meaning Facet is a key aspect of meaning, both in terms of the phenomenon itself and
1052 discussions about it. This facet also readily extends to study of non-human signal forms. We
1053 illustrated this throughout this section using examples from dwarf mongoose alarm calls to
1054 whale song, highlighting their signal content and form, and apparent literal surface signal
1055 meanings. This in spite of the fact that the Signal Meaning Facet is mostly studied by human-
1056 centric scholars, as part of countless studies of *semantics*.

1057

1058 **V. INTERACTANT MEANING FACET**

1059 The second global meaning facet, the Interactant Meaning Facet (a and c in Fig. 1), focuses
1060 on how the communicative interactants as well as context shape a signal's meaning. It loosely
1061 relates to Austin's (1975) illocutionary speech acts, as well as the joint action and user-
1062 centred approach taken in the communication model developed by Clark (1996). Here,
1063 meaning arises from an (inter)active process. Where the signaller intends to convey a
1064 meaning, and/or where a perceiver infers or conceptually creates a meaning from an
1065 interaction or a situation, this meaning facet pertains to qualities of the interactants rather
1066 than the signal. It corresponds to a Tinbergian survival value or function (Tinbergen, 1963),
1067 in terms of focusing on interactions that can carry proximal benefits from intentional
1068 signalling for instance and is characterised by the dynamic cognitive processes of signallers

1069 and perceivers. An example within non-human communication is how different species
1070 engage in active turn-taking (e.g. Pika *et al.*, 2018). In such systems like turn-taking
1071 involving flexibility, timing, and various responses, which are increasingly being studied
1072 comparatively (Heesen *et al.*, 2022), we can see how interactive, collaborative
1073 communicative meaning seems to arise in another species and thus illustrates this meaning
1074 facet.

1075

1076 **(1) Importance of communicative collaboration**

1077 For an understanding between individuals to occur, communicative collaboration is
1078 necessary. Thus, Lewis' (1986) work on conventions contained a model of behavioural pairs
1079 that make and interpret signs, illustrated with the example of the eighteenth-century
1080 American Revolution Patriot Paul Revere's simple lantern code. One lantern would be lit if
1081 the enemy came by land, two if they came by sea. Where the behaviours are stable, they can
1082 develop into conventions for sharing common interests. Skyrms (2010) then generalised this
1083 model by showing how signals can evolve by natural selection as well as how they can be
1084 chosen by agents (Artiga *et al.*, 2020), where the production of signals becomes shaped by
1085 their interpretation and *vice versa*.

1086 Planer & Godfrey-Smith (2021) show how meta-semantic traditions fall into two categories:
1087 an expressive tradition where meaning is thought of as concepts that signallers are trying to
1088 convey or behaviour they are trying to influence, and an interpretative tradition where
1089 meaning is based on perceivers' interpretation of signals. Thus, both production and
1090 perception must be considered. Indeed, as Steinert-Threlkeld, Schlenker & Chemla (2021)
1091 note, there is symmetry between the signal causation and the resultant action, which is why
1092 Macedonia & Evans (1993) include both a production and a perception criterion in their
1093 functional reference definition. Seyfarth & Cheney (2003), on the other hand, do not

1094 incorporate such collaboration in their model, focusing instead on there being simply calls in
1095 response to stimuli and, separately, a perceiver extracting information, as more aligned with
1096 the notion of *cues* rather than active *signals*. They note: “Although listeners acquire rich
1097 information from a caller's vocalisation, callers do not, in the human sense, intend to provide
1098 it. Listeners acquire information as an inadvertent consequence of signaler behavior”
1099 (Seyfarth & Cheney, 2003, p. 33). This, however, does not appear to be the case for grouper
1100 fish (*Plectropomus pessuliferus marisrubri*) and coral trout (*Plectropomus leopardus*) that
1101 regularly point out prey hiding in crevices to other local predators with distinct vertical
1102 headshakes, and even a horizontal ‘shimmy’ to recruit these other predators to hunt (Vail,
1103 Manica & Bshary, 2013).

1104

1105 **(2) Interactant S and P Meaning Facets**

1106 This discussion about distinguishing signallers and perceivers leads to two subdivisions: an
1107 *Interactant S(ignaller) Meaning Facet* (a in Fig. 1) and an *Interactant P(erceiver) Meaning*
1108 *Facet* (c in Fig. 1). Within the Interactant S Meaning Facet, we can discuss the possibility and
1109 degrees of signaller intentionality, including Grice’s (1957) overt intentionality to make it
1110 clear to perceivers that the signaller is both communicating and intends to communicate. This
1111 facet also includes discussion of theory of mind, and the understanding and manipulating of
1112 such communicative intentionality and any triadic reference that may be communicated
1113 (Tomasello, 2003), which would include deception.

1114 The Interactant P Meaning Facet involves interactant asymmetries for those who argue that
1115 the onus lies with the perceiver to extract information, as well as inferences about signaller
1116 intentions and specific content (Bar-On & Moore, 2017). We can also discuss the role of
1117 mental representation and how this contributes to meaning, both in terms of Saussure’s
1118 (1966) point that meaning resides in the minds of speakers and hearers, and in terms of what

1119 perceivers add to meaning construction. For instance, Smith (1977, 1997) distinguishes
1120 *messages*, with information encoded by a signaller, from *meaning* as the information a
1121 perceiver derives from a signal along with context. Another example is within interactive
1122 conversational repair that occurs where meaning temporarily breaks down for humans
1123 (Dingemanse, Blythe & Dirksmeyer, 2018). Such repair occurs through, for example, using
1124 question words like ‘What?’ or interjections like ‘Huh?’

1125 Other considerations within the Interactant P Meaning Facet include the notion that
1126 perceivers focus not on the speaker’s actual intention but their *apparent* intention, and what is
1127 interpreted by the perceiver despite any mistakes for instance on behalf of the signaller (Leth,
1128 2021). Moreover, audience effects (e.g. Demartsev *et al.*, 2014) and any familiarity between
1129 signallers and perceivers “are not yet well studied or understood for most systems, but are
1130 likely to increase the complexity of communicative interactions even further” (Higham &
1131 Hebets, 2013, p. 1386). Therefore, communicative context and the circumstances of
1132 production and perception of a signal are equally important for their contribution to the
1133 meaning of the communication (Macedonia & Evans, 1993).

1134 Unlike the nature of the communicative signal, or the outcome of the communication, each of
1135 which are dealt with by the other two meaning facets, the interactants and the context in
1136 which they interact contribute to the communicative meaning in a very different way.
1137 Martínez (2019) argues for a strong isomorphism where signallers and perceivers are
1138 involved in a signalling game and jointly manage an information-processing channel.
1139 Moreover, as Bateson (1966, p. 574) states, “We shall not know much about dolphin
1140 communication until we know what one dolphin can read in another’s use, direction, volume,
1141 and pitch of echolocation”. Thus, the Interactant Meaning Facet is a key facet in this
1142 theoretical framework, which can be applied across species. It also shows, as discussed in
1143 earlier sections, how meaning is a dynamic rather than a static phenomenon.

1144

1145 **VI. RESULTANT MEANING FACET**

1146 Finally, the Resultant Meaning Facet focuses on the outcomes of a communicative situation.

1147 This facet of meaning loosely relates to Austin's (1975) perlocutionary speech acts. So,

1148 within interactions, one person can make a statement that implies action for another person

1149 and the perceiver can either acknowledge the meaning of the statement, corresponding to

1150 successful information transfer, or acknowledge their need to adapt their behaviour,

1151 corresponding to behavioural influence. In both cases, uptake of meaning and

1152 acknowledgment are key to the success of the communication, referred to here as *outcomes*.

1153 This facet is especially important for studying non-humans, because our window into their

1154 minds is limited, although their behaviour and communicative outcomes are readily apparent.

1155 Even so, the salient point made by citing Austin is that this facet pertains just as much to

1156 human interactions, even if it is not so commonly studied.

1157 The Resultant Meaning Facet focuses on the benefits or meaning uses for the communicative

1158 interactants, especially but not limited to the signaller. From a functional and evolutionary

1159 standpoint, as per Tinbergen (1963), a signal can only be adaptive and thus passed on across

1160 generations if it accrues benefits for the signaller by maximising (inclusive) fitness. A non-

1161 human example might be an automatic, reactive, and affective growl that warns away other

1162 animals from stealing food. Any deceptive signal would also belong to this category. It is

1163 necessary for signallers to benefit from producing signals, otherwise the signals would not

1164 increase fitness and might be eliminated by selection. Perceivers do not need to benefit from

1165 signals in the same way, although on balance it may be that perceivers do also benefit in a

1166 majority of cases, which would help support the longevity of particular signals. This

1167 discussion creates two subdivisions of this meaning facet: a *Resultant Meaning Facet* (d in

1168 Fig. 1) for signaller benefit only and a *Resultant Mutualistic Meaning Facet* (e in Fig. 1)
1169 where both interactants benefit from the signal.

1170 The Resultant Meaning Facet occurs where perceiver responses are coherent with the signal.
1171 This means that the behavioural outcomes are consistent with what might reasonably be
1172 expected of the signal itself and the signaller's meaning and intention, whether the signal is
1173 deemed informative and/or influential. This is consistent with Hobaiter & Byrne's (2014)
1174 approach to determining chimpanzee gesture meaning *via* "apparently satisfactory
1175 outcomes", where the cessation of gestures upon plausibly desired conspecific responses
1176 appears to demonstrate the intended meaning of the gestural signal. However, it should be
1177 noted that there is a methodological limitation involved here, whereby behavioural responses
1178 can only highlight an imperative signal, one making a demand or request of a perceiver,
1179 rather than a declarative signal that can be harder to detect within the communicative
1180 interaction (Hobaiter, Graham & Byrne, 2022).

1181 From an evolutionary standpoint, where perceiver responses are not consistent with the
1182 signal, the signal may be deemed meaningless, but only in terms of the outcomes of the
1183 communicative interaction, or the Resultant Meaning Facet as per our terminology. This is
1184 because, regardless of any meaning contained within or surrounding the signal, or intended
1185 by the signal, if the signal fails to change others' actions in a manner consistent with the
1186 signal it could be argued that the ultimate outcome gives the signal no adaptive value. An
1187 example would be if no animal responds to a threat display, or if an animal responds in a way
1188 that is inconsistent with a show of aggression from the signaller. These signals may well die
1189 out, even though meaning may have been involved in the signal itself and in the signaller's
1190 intentions. The signal may still refer to an entity or the signaller may intend to influence a
1191 perceiver, but the outcome does not align with the signal and/or the signaller, and so the
1192 overall meaning of the signal is lost and the particular signal cannot further evolve.

1193 Returning to the newspaper example mentioned in Section II.3, the redundancy of the old
1194 news to a particular reader leads to a loss of the meaning of the newspaper in terms of the
1195 outcome, since the news is not new for the reader and the reader will therefore not act upon
1196 the information in a way consistent with the news or the writer's intentions. However, what is
1197 written and the intentions behind the writing remain the same, and therefore must be dealt
1198 with separately with respect to each of the three meaning facets. Thus, it is important to note
1199 that meaning still exists within the newspaper from the writing itself and the intentions
1200 behind the writing, but that it does not arise within the outcomes of the communication. A
1201 newspaper is a complex example, though, because it is written for a readership of more than
1202 one person, so the majority of perceivers may in fact find the news contained within to be
1203 noteworthy.

1204 A further point to make here is that any notable lack of consistency in outcome with the
1205 signal must derive from a breakdown in signal form, content, or interactant cognitive
1206 processes, rather than a simple unwillingness of a perceiver to cooperate, perhaps due to an
1207 individualistic tendency simply to be uncooperative, which would have no overall impact on
1208 signal effectiveness. A linguistic example of such a meaning breakdown in terms of outcomes
1209 would be communication with someone who has Wernicke's aphasia. This is a specific
1210 localised brain damage that affects speech, where the person with the aphasia struggles to
1211 understand others' language use and often strings together sentences that are (mostly)
1212 grammatical but make no sense (e.g. Greenwald, 2018).

1213 Where there is mutualistic (cooperative) communication, perceivers may also benefit
1214 simultaneously with signallers. A non-human play signal can invite a conspecific to engage in
1215 joviality and practice sparring, which involves real-time benefit for both parties. Human–
1216 wildlife mutualisms form another example, like the honeyguide bird (*Indicator indicator*)
1217 leading humans to beehives to share the spoils (Spottiswoode, Begg & Begg, 2016).

1218 Sometimes the benefits can be delayed to one or both parties, as with altruistic behaviour.
1219 Helping a vulnerable party that is not kin, especially if they are of another species (e.g.
1220 dolphins saving floundering human swimmers; Gregg, 2013), can seem like a waste of
1221 precious resources. However, altruism can lead to reciprocal altruism (e.g. rats aiding other
1222 begging conspecifics, whose actions are then reciprocated; Paulsson & Taborsky, 2021),
1223 cooperative problem solving or hunting, or kin benefits. This can therefore increase an
1224 individual's lifespan or create greater environmental 'harmony' which may benefit all
1225 involved.

1226 Therefore, meaning not only arises from the signal itself, or just from the communicative
1227 interactants and their context, but also from the outcome(s) of the communication. These are
1228 not different meaning types, but all different facets of one meaning phenomenon that arises in
1229 a communicative setting. Therefore, the Signal Meaning Facet, the Interactant Meaning
1230 Facet, and the Resultant Meaning Facet are all integral to describing meaning across
1231 disciplines and species (Fig. 1).

1232 Furthermore, the above outcome examples avoided linguistic examples, to ensure that there is
1233 no conceptual conflation with semantics that would be involved in the Signal Meaning Facet,
1234 while specific mention of intentionality has also been avoided to highlight the distinction
1235 from the earlier Interactant Meaning Facet. Although these aspects are all very common
1236 across communication systems, the important point to note is that the three facets are separate
1237 from one another. The facets can easily be combined, and a clear example would be someone
1238 telling their romantic partner, 'I love you', which involves semantic and pragmatic reference,
1239 a specific context, intentional overt meaning implications, affective communication, and
1240 behavioural influence on a perceiver that (hopefully) benefits both parties. Yet, the three
1241 meaning facets must be differentiated similarly to the way that Austin (1975) separated
1242 denotation from connotation and outcomes within his speech act theory. This differentiation

1243 permits the systematic investigation of each meaning facet across species, even where some
1244 aspects of each of the facets remain in dispute, as well as giving clarity over which facet of
1245 meaning is being discussed at any one time.

1246

1247 **VII. WORKED NON-HUMAN EXAMPLE OF THE THREE MEANING FACETS**

1248 Now that the three key meaning facets have been described, we present a brief worked
1249 example of how this framework can be applied to an instance of non-human communication,
1250 especially one that exhibits all three of the meaning facets. The communication we focus on
1251 is the ‘jump–yip’ display of black-tailed prairie dogs (*Cynomys ludovicianus*). Individuals of
1252 this species instigate a contagious signal (one spreading throughout the group) as a form of
1253 contact calling: a jump–yip display, involving a call and a physical movement, to assess the
1254 alertness of others in the group (Hare, Campbell & Senkiw, 2014). In terms of the Signal
1255 Meaning Facet, it is possible to study the acoustic modality features of the signal combined
1256 with the upward leap of the body (e.g. Smith *et al.*, 1976), as well as the reference aspect
1257 associated with the call, reaching out to others in the group. Regarding the Interactant
1258 Meaning Facet, we can focus on the contagious nature of the signal and how it spreads
1259 throughout a group (Hare *et al.*, 2014), with apparent turn-taking and multimodality aspects
1260 to consider, as much as how it can be used in diverse contexts, from startled individuals to
1261 territorial defence (Smith *et al.*, 1976), and also considerations of the signaller intentions and
1262 perceiver inferences involved. Lastly, in terms of the Resultant Meaning Facet, we can
1263 consider Hobaiter & Byrne’s (2014) “apparently satisfactory outcomes”, given that the initial
1264 jump-yipper stops signalling once the other members of the group respond with the signal.
1265 This Mexican wave-like signal (Hare *et al.*, 2014) demonstrates the signaller’s apparent
1266 intention to establish contact with conspecifics, which ceases once that contact has been
1267 established with the perceiver response signals, and the initial signallers often return to

1268 foraging. Given that all three meaning facets can be described within this one type of
1269 signalling event, this would be a clear candidate for being termed meaningful non-human
1270 communication.

1271

1272 **VIII. LESSONS FROM NON-HUMAN COGNITION AND LINGUISTICS**

1273 As can be seen from discussions in the literature and our summative framework, the cognitive
1274 underpinnings of meaning are already recognised across species. There is also growing
1275 acceptance that language, closely linked to meaning, could have had its origin in non-human
1276 cognition and was exapted for communication by humans (Amphaeris, Shannon & Tenbrink,
1277 2021; Bickerton, 1990; Fitch, 2019; Reboul, 2017). Even the recent Cognitive Discourse
1278 Analysis methodology (Tenbrink, 2020) centres around using what people say to explore the
1279 inner workings of their thoughts, which is linked to the more general cognitive- and meaning-
1280 based approach to language in the cognitive linguistics movement (e.g. Evans & Green,
1281 2005). Non-human communication evokes a different reaction. Consideration of its
1282 complexity or involvement of meaning is tempered by the contentions over non-human
1283 communication's link to language, which is widely deemed to be uniquely human, a view
1284 championed by linguist Chomsky (1965 and onwards). However, a recent Prototype-Theory
1285 based – continuous rather than discrete categorisation, or 'fuzzy boundaries' – approach to
1286 the conceptualisation of language and the integration of non-human communication features
1287 (Amphaeris, Shannon & Tenbrink, 2022), demonstrates a strong theoretical overlap across
1288 species for such phenomena, like language. This approach could also include meaning, a
1289 concept closely linked to language and just as complex. Additionally, such a theory that
1290 integrates non-human communication into the contentious concept of language can only
1291 facilitate a slightly more palatable concept of non-human communicative meaning. Thus, not
1292 only is there a conceptual option for a species overlap rather than distinction regarding

1293 communication and language, but there is also broader acknowledgement that at least non-
1294 humans have the cognitive capacity for meaning, so that past limited assumptions about non-
1295 human communication need not be upheld.

1296 Moreover, the analysis of meaning in Sections II–VI has been important, not just to
1297 substantiate and make explicit the importance of the growing tendency in the literature to
1298 acknowledge that meaning is a complex multifaceted concept, but also to demonstrate how
1299 non-human communication exhibits each of meaning’s three different facets, at least to a
1300 degree, among some species. However, this very point – that non-humans exhibit these facets
1301 – begs the question: why do we still question meaning in non-human communication?

1302 Whether or not we can only apply the term *meaning* to communication that exhibits all three
1303 facets simultaneously, clearly multiple species are involved in at least one meaning facet
1304 discussion and at least some species exhibit all three meaning facets. This is based simply on
1305 what science has discovered so far about both non-human communication and about the
1306 facets of meaning. We therefore suggest revisiting the term *non-human/animal*
1307 *communication*, which subsumes hundreds of thousands of diverse species, and obscures any
1308 understanding of the variations among them. With all these approaches in mind, furthermore,
1309 we have shown that the multifaceted approach establishes the presence of at least aspects of
1310 meaning in non-human communication. By doing so, we have progressed beyond
1311 Kershenbaum *et al.*’s (2016) observation of the lack of agreement over the nature of meaning
1312 and the disconnect between theories of human semantics and animal communication because
1313 our framework can be applied consistently across all species.

1314

1315 **IX. CONCLUSIONS**

1316 (1) Herein, we have created a framework to bring structure and coherence to the
1317 interdisciplinary interspecies discussions of meaning.

1318 (2) We have made explicit the importance of a growing tendency in the literature towards the
1319 multifaceted nature of meaning. As such, we have shown that meaning does not require
1320 multiple definitions and that there are not different types of meaning, but rather that meaning
1321 itself is multifaceted. Meaning has different aspects that must be accounted for in a coherent
1322 framework, and they need to be carefully aligned in comparative studies.

1323 (3) We have highlighted that, beyond any cognitive underpinnings of meaning already
1324 recognised across species, by exploring the multifaceted nature of meaning, as well as by
1325 adapting a recent continuous categorisation-based approach in linguistics to the
1326 conceptualisation of complex concepts like language or meaning, we have discovered there is
1327 potentially much more overlap in meaning across species than hitherto acknowledged.

1328 (4) Moreover, all three of the meaning facets proposed in our framework are clearly found
1329 within the languages of humans and seem also to exist to varying degrees among at least
1330 some non-humans. The Signal Meaning Facet arises in non-human communication when
1331 exploring how signals are encoded in different ways. The Interactant Meaning Facet
1332 incorporates discussion of non-human cognition, inference, and communicative intentional
1333 behaviour. The Resultant Meaning Facet may involve information transfer and/or merely
1334 behavioural influence, but in any case allows us to concentrate on the exact nature of how
1335 signals accrue their adaptive benefits. There are even instances like the jump-yip display of
1336 black-tailed prairie dogs that demonstrate all three of the facets together. Therefore, we are
1337 indeed talking about *meaning* when we talk about non-human communication, at least for
1338 some animals and to some degree. We suggest that it is time for this term to be used and the
1339 phenomenon to be studied more by ethologists, evolutionary biologists, and researchers in
1340 other related fields.

1341 (5) Applying a multifaceted approach to non-human communication research can inform and
1342 resolve key debates in the field because non-human communication data sets are growing

1343 rapidly with improved equipment, automated recording, and new quantitative approaches for
1344 data analysis. It is important that researchers can leverage these data with an integrated
1345 approach, so that non-human communication evidence may be interpreted more
1346 comprehensively and be compared to language(s) more effectively. Functionalist perspectives
1347 that emphasise the role of meaning within language can benefit from this framework too,
1348 because it is essential to understand the origin and nature of meaning for how it impacts on an
1349 understanding of the evolution and nature of language and communication, the study of all of
1350 which will from now on need to involve non-humans more centrally.

1351 (6) Whether this framework moves us any closer to understanding the nature of meaning
1352 itself as an epistemological phenomenon is beyond the scope of this review. Nevertheless, we
1353 place the use of the term *meaning* on a firmer and more coherent theoretical basis than
1354 available before, with a multifaceted framework that connects disciplines and species. This
1355 enables a closer examination of the evolutionary transition(s) from communication in early
1356 non-humans and early hominids to the richness of language and what we are discovering of
1357 contemporary non-human communication. Researchers can now focus on the specific nature
1358 of that meaning, including the rich granularity to which it might extend. Most importantly,
1359 they can seek to gather further non-human communication data knowing that findings may
1360 involve much more meaning than just scholarly interpretation.

1361

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1367

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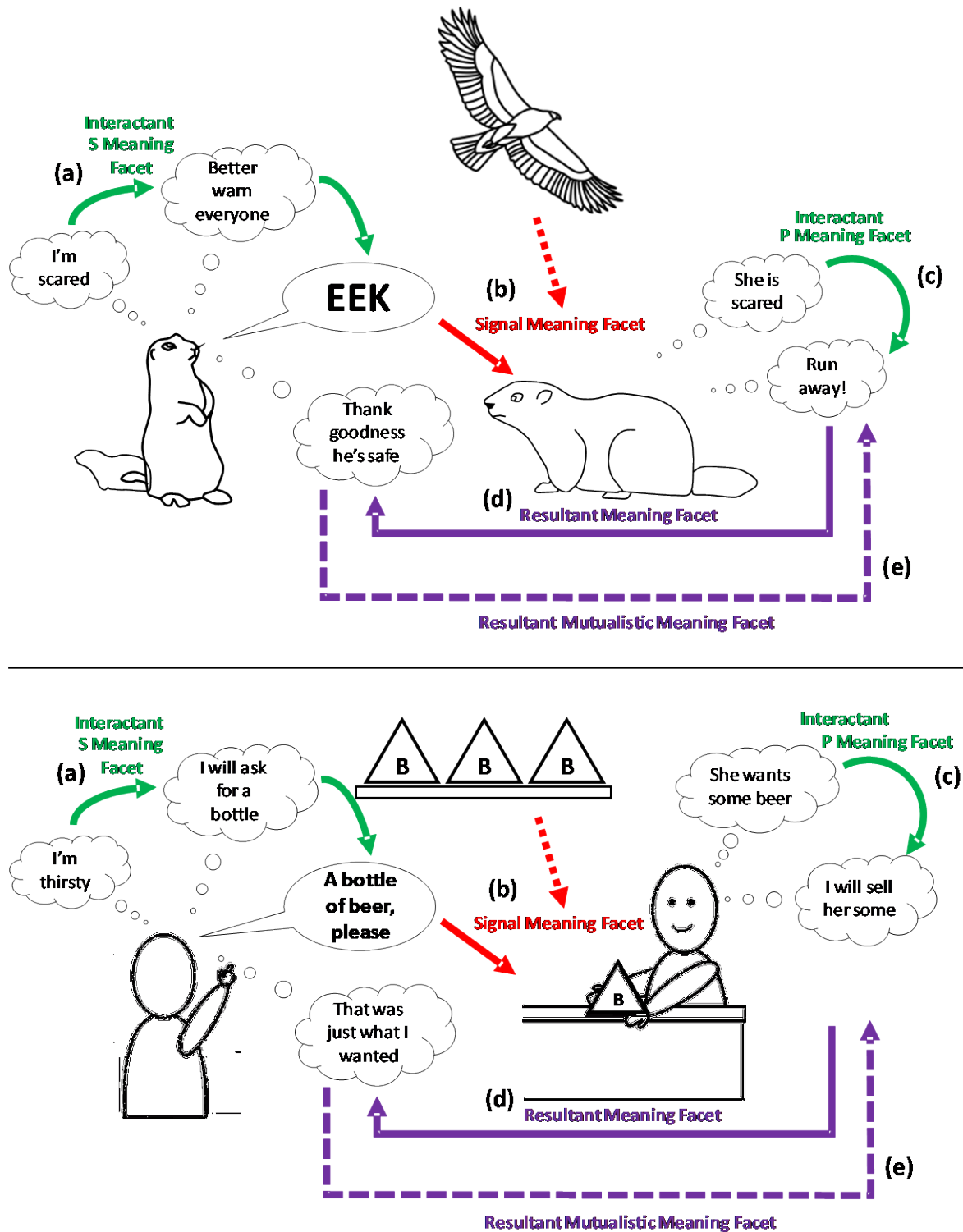
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1747

1748 **Table 1.** Application of Austin's (1975) speech act analysis to meaning study.

Non-humans	Both occur in comparisons of non-human communication to language		Often occurs when non-human communication is studied per se without human comparison
	Reference in non-human communication debate	Intentionality in non-humans debate	Information transfer or behavioural influence debate
	Relates mainly to Tinbergian mechanisms	Relates mainly to Tinbergian function	Relates mainly to Tinbergian ontogeny, and evolutionary fitness benefits (at least for signallers)
	Locutionary Act: surface meaning	Illocutionary Act: implied meaning	Perlocutionary Act: meaning outcomes
	Relates to discussions about denotation, conventional semantics, sense and referents, communication models and affect. May take the (linguistic) sign form of icons, indexes, symbols, or paralinguistic communication	Relates to discussions about connotation, context-based pragmatics, Grice's overt intentionality, and inference	Relates to outcomes of communicative interactions separate to the apparent meaning or intention/inference of signals
Humans			

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1752 **Fig. 1.** How meaning arises between individual non-humans (upper) and humans (lower).

1753 The figure illustrates how meaning may be understood to arise in human and non-human

1754 communication. (a) The signaller's cognitive processes motivate a communicative signal, the

1755 *Interactant S Meaning Facet*. (b) This signal occurs *via* a communicative modality (e.g.

1756 acoustic), and co-relates (or refers) to an external stimulus (e.g. the eagle), which is part of
1757 the *Signal Meaning Facet*. (c) The perceiver interprets the signal and forms a cognitive
1758 inference and interpretation, the *Interactant P Meaning Facet*, which may or may not fully –
1759 but must partially – correspond to the *Interactant S Meaning Facet*. (d) The behaviour of the
1760 perceiver is altered in a way that produces the result desired/evolutionary outcome required
1761 by the signaller, which is the *Resultant Meaning Facet*. (e) In the case of mutualistic
1762 interactions, there may also be correlation between the goals of the signaller and perceiver, a
1763 *Resultant Mutualistic Meaning Facet*, with the roles being reversible, as is common in human
1764 dialogue. Here, mutual understanding is frequently signalled from both sides: ‘Shall we go
1765 for a walk?’–‘Yes’–‘Good’.
1766