BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Biol. Rev. (2023), **98**, pp. 1887–1909.
doi: 10.1111/brv.12989

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

Jenny Amphaeris[1,*], Daniel T. Blumstein[2], Graeme Shannon[3], Thora Tenbrink[1] and Arik Kershenbaum[4]

[1]*School of Arts, Culture, and Language, Bangor University, College Road, Bangor, LL57 2DG, UK*
[2]*Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA*
[3]*School of Natural Sciences, Bangor University, College Road, Bangor, LL57 2DG, UK*
[4]*Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK*

ABSTRACT

Does non-human communication, like language, involve meaning? This question guides our focus through an interdisciplinary review of the theories and terminology used to study meaning across disciplines and species. Until now, it has been difficult to apply the concept of meaning to communication in non-humans. This is partly because of the varied approaches to the study of meaning. Additionally, while there is a scholarly acknowledgement of potential meaning in non-human cognition, there is also scepticism when the topic of communication arises. We organise some of the key literature into a coherent framework that can bridge disciplines and species, to ensure that aspects of meaning are accurately and fairly compared. We clarify the growing view in the literature that, rather than requiring multiple definitions or being split into different types, meaning is a multifaceted yet still unified concept. In so doing, we propose that meaning is an umbrella term. Meaning cannot be summed up with a short definition or list of features, but involves multiple complexities that are outlined in our framework. Specifically, three global facets are needed to describe meaning: a *Signal Meaning Facet*, an *Interactant Meaning Facet*, and a *Resultant Meaning Facet*. Most importantly, we show that such analyses are possible to apply as much to non-humans as to humans. We also emphasise that meaning nuances differ among non-human species, making a dichotomous approach to meaning questionable. Instead, we show that a multifaceted approach to meaning establishes how meaning appears within highly diverse examples of non-human communication, in ways consistent with the phenomenon's presence in human non-verbal communication and language(s). Therefore, without further recourse to 'functional' approaches that circumvent the critical question of whether any non-human meaning exists, we show that the concept of meaning is suitable for evolutionary biologists, behavioural ecologists, and others to study, to establish exactly which species exhibit meaning in their communication and in what ways.

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

CONTENTS

* Author for correspondence (Tel.: +01248 351151; E-mail: j.amphaeris@bangor.ac.uk).

I. INTRODUCTION

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

Until now, it has been difficult to apply the concept of meaning to non-humans, especially their communication, partly because of the varied approaches to the study of meaning and lack of the concept's definition. Additionally, while there is some scholarly acknowledgement of the relevance of meaning in non-human cognition, there is also considerable scepticism when the topic of communication arises. Such scepticism comes from a reluctance to assume intentionality in non-humans, and also where contentious comparisons are made between language(s) and the communication systems of non-humans (topics raised by Scott-Phillips, 2015). Thus, there is often recourse to 'functional' interpretations of non-human communication, such as with the proposal of 'functional reference' (Macedonia & Evans, 1993), to acknowledge aspects consistent with human communication but simultaneously to circumvent the complicated question of whether non-human meaning exists. We aim to review and organise key literature in the meaning landscape into a coherent framework that can bridge disciplines and species, to ensure that aspects of meaning are being accurately and fairly compared. We also advance an understanding of meaning by highlighting that, to study meaning, we must adopt a multifaceted perspective. Our comparative framework aims to enable researchers to recognise various aspects of meaning in non-human communication, a term which encompasses at least hundreds of thousands of animal species other than humans (Mora *et al.*, 2011), and so involves an impressive diversity that challenges a simple dichotomous human/non-human perspective.

Our contribution is similar to Berthet *et al.*'s (2023) animal linguistics primer. We deal with the same challenges of interpreting non-human communication, but we provide a more expanded insight into meaning than the definition that Berthet *et al.* (2023, p. 83) propose: 'The set of features of circumstances that appear at a rate greater than chance across the signal's occurrences'. In doing so, we also make explicit the importance of the growing view that, rather than requiring multiple definitions or being split into different types, meaning should be viewed as a multifaceted concept. We outline three global facets that arise from a

synthesis of the literature: a *Signal Meaning Facet* pertaining to the nature of the communicative signal itself, an *Interactant Meaning Facet* pertaining to the motivations and inferences of the interacting communicative participants and the situational context, and a *Resultant Meaning Facet* pertaining to the outcome of the communicative signal and signaller–perceiver interaction, along with their theoretical basis and terminology. Throughout, we also consider Tinbergen's (1963) four questions for studying animal behaviour: mechanisms (causation), ontogeny (development), function (survival value), and evolutionary history, and the need to explain the concept of meaning in terms of its adaptive value, without which it would not have arisen at all. We also highlight recent research demonstrating how non-human communication may be integrated into a concept of language through the perspective of continuous rather than discrete categorisation of abstract concepts like language. This inclusive approach could be extended to meaning as well. Ultimately, we argue that such a combined multifaceted and continuous categorisation approach establishes the justification for applying the concept of meaning to at least some instances of non-human communication. This has strong implications for the study of the nature of meaning, language, and non-human communication combined, as well as a richer understanding of the evolutionary pathways involved.

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

Throughout, we make use of many examples based on human experience, as the reader may find the intention of the communicative act, and the perception of that act, easier to understand. Moreover, it helps to elucidate the comparatively smaller repertoire of documented intentional communication amongst non-humans, as well as allowing for the fact that cognitive processes may differ across species, which is a flourishing area of research.

A final necessary caveat is the matter of terminological definitions in two respects. First, we must note the complexity involved in each area of this research, each leading to its own avenue of detailed debates. We have therefore adopted working definitions and examples throughout to attempt to streamline these complex issues, present a single perspective on each of the topics, and maintain focus on how to unify all the key concepts relating to meaning into a framework that can be applied across disciplines and species. Second, we note that linguistic terminology borrowed by comparative researchers may sometimes be applied to other species without clear definition or description of how the concept is being operationalised, so that terminology may be used differently in various studies. Again, our framework assists the comparative approach to give greater consistency and clarity over which aspects of meaning are being explored for a given species.

II. THE THEMES OF MEANING

This section discusses key themes that arise in the interdisciplinary literature. Firstly, there is the role of mental representations, the 'having of concepts', which are fundamental units of knowledge analysed from perceptual experience (Evans, 2007), and without which there can be no meaning. This leads naturally into a discussion of reference, which connects mental meaning with the world and is also the most observably meaningful part of communication, our main focus here. However, a serious confound must then be addressed concerning four competing ways in which the term *semantics* is used. Another prominent aspect of the study of meaning – the content of meaning, which connects with our need to explain the adaptive value of meaning (Tinbergen, 1963) and how it evolved – can be summed up with the question: what does meaning achieve? The best-known theories ascribe to meaning the role of reference, information transfer and/or influencing behaviour, and the conveying and recognition of communicative intentions, which are all dealt with in separate subsections. Lastly, there are theories that point to the multifaceted nature of meaning, although without making the importance of this point explicit in itself. We will argue that this point is crucial to a more in-depth understanding of meaning and where it can be found across species. We consider five topics: mental representations, semantics, referencing information or manipulating behaviour, communicative intentionality that supports such reference or manipulation, and multifaceted theories of meaning. These topics provide the reader with an overview of the key debates and a thematic summary of how meaning has been treated in the literature so far. This establishes a firm foundation upon which our cross-species meaning framework can be built.

(1) The role of mental representations

From the perspective of studying humans at least, meaning is closely related to the notion of mental representations, which is how concepts intervene between perception and responses and can be built from perception of the real world or other imagined/stored concepts. This addresses the cognitive dimensions of meaning. This notion of mental representations and a consideration of real and conceptual entities partly aligns with the semantic/pragmatic distinction, which is based upon whether an actual context is involved in a perceived/imagined situation. Mental representations also align

with reference, which requires meaning in the mind to be separated from the objects and contexts observed in the real world. Thus, Frege's (1948) dualistic notion of *sense* emphasises the 'cognitive value' counterpart to a hypothetical or real-world referent within meaning's *reference* (a cognitive means of indication).

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

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

Indeed, the notion of signalling being inherently honest without manipulation, perhaps due to signalling costs of deception in evolutionary terms, is discussed both with respect to human communication (e.g. Buller & Burgoon, 1996) and in the evolutionary biology literature (e.g. Whiten & Byrne, 1988), in terms of the usefulness and legitimacy of a signal for signallers and perceivers (e.g. Akçay *et al.*, 2013), as well as unambiguous manipulation. Early studies tended to claim that only honest signalling is possible within non-human communication (Rowell *et al.*, 2006). However, beyond any possible misinformation transfer or error in signalling, deception may also occur in non-human communication, as a strategic interaction. There are multiple acknowledged Machiavellian behaviours in the animal kingdom (e.g. Byrne & Whiten, 1988; Knight, 1998), such as 'social tool use' in chimpanzees (*Pan troglodytes*) that manipulate others to obtain a food source (Schweinfurth *et al.*, 2018), and fork-tailed drongos (*Dicrurus adsimilis*) that utter false alarm calls to scare other animals from their food source to steal it (Flower, Gribble & Ridley, 2014). These communicative behaviours could fulfil the requirement of Adams & Beighley (2013) that true *prevarication* is possible only after a concept of deceit has been established in the mind of the signaller, which the alleged presence of mental representations in other species would support.

Some game theorists argue that the content or meaning of a signal derives specifically from contexts of collaborative common interest (Skyrms & Barrett, 2019), and this is explicitly in the form of honest signalling, even for humans. One example the authors give is that the brand name 'Louis Vuitton' derives its meaning and societal value from 'honest' authentically made and therefore common interest/collaborative products like suitcases. The meaning associated with the brand name 'Louis Vuitton' would hold even if most items in the world bearing the name Louis Vuitton were found to be fake, because the meaning arises from the honest signal, here the genuine label name. Grice's (1975) cooperative principle also describes how humans make their conversational contributions appropriate to the situation in terms of four maxims: the *quantity* of information is relative to what is required, there is a truthful and adequately evidenced *quality* of contributions, which are *relevant*, and are contributed in a *manner* that offers clarity, brevity, and order. This principle therefore lists honesty as a principle underlying effective human communication. Yet, regardless of which is the more effective evolutionary strategy, deception also abounds across species, as a potential indication of mental representation in humans and non-humans alike. Given the strong associations between mental representation and meaning topics like reference, as well as the increasing supportive evidence for mental representations in non-humans, this indicates that meaning is cognitively possible for non-humans, potentially also within their communication.

(2) Reference, semantics, and pragmatics

(a) *Reference and semantics*

The discussion of the mental representation and cognitive aspect of meaning, touching on reference, leads naturally to a discussion of reference in more depth, because this is where meaning connects most observably with communication. However, to move forward with the literature review and the framework we are constructing, we must first discuss how semantics is used. *Semantics/semanticity* can be used as a term to discuss meaning generally, and is used extensively within human centric scholarship, as well as increasingly in non-human communication literature (e.g. Seyfarth, Cheney & Marler, 1980; Suzuki, Wheatcroft & Griesser, 2020). However, semantics is often used as a heading for its three associated phenomena, which are three distinct ways in which meaning can be conveyed within and in addition to a signal across species: reference or sense and referent relations (Frege, 1948), the

three sign forms (Peirce, 1984) – especially symbols (Saussure, 1966), and context (or more specifically independence from context, as opposed to context-based *pragmatics*). We will now explore these three often-conflated associations with *semantics*.

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

As its second more distinct usage, *semantics* is often linked to symbolic signs too. Peirce (1984) noted that there is a triadic set of forms that a sign may take: icons or 'likenesses', for instance when we outline the shape of a box with our hands; indexes, in which signs in some way directly correspond to real objects, like a pointed finger guiding one's attention, as with African savannah elephants (*Loxodonta africana*) guided to food (Smet & Byrne, 2013); and lastly symbols, which are conventional form-meaning pairings, as used in written numerals and religious or political emblems in art. The meaning-specification role of semantics is thought to occur predominantly within a symbolic system (Speaks, 2021) because the 'definite' fixed pairing of a sense with a referent (Frege, 1948) appears to correspond to conventionalised form-meaning pairings that characterise symbolic signs (e.g. Deacon, 1997). We purposefully avoid stating that symbols are *arbitrary* form-meaning pairings, as proposed by Saussure (1966), because we will shortly address this point in the third connection to semantics, the role of context, and because not everyone agrees with the prominence of the arbitrary quality of symbols. Deuchar (1996), for instance, argues that conventionality is more integral than arbitrariness, because not all language is arbitrary, and because, although arbitrariness tends to happen naturally over time (Watson *et al.*, 2022), conventionality is the crucial aspect for symbol creation and usage.

The semantic–symbolic connection is also supported by the proposed context-independent nature of semantics and an alleged arbitrariness of symbols (Saussure, 1966), which is the third more distinct use of the term *semantics*. Where communication is concerned, much of the literature tends to separate out *semantics* from *pragmatics* (e.g. Devitt, 2021; Gutzmann, 2020). This distinction relates to the frequently held notion that semantic signals can be thought of in terms of either a conventional meaning independent of any context (a situated instance), or pragmatically in terms of the ways in which the signals exceed their conventional meaning in a specific usage situation. This could include novel use or stretching the scope of a word like 'interesting', which caters not only for describing genuinely intriguing topics but also topics we politely have to suffer for a friend. This semantic–pragmatic distinction also relates to the difference between *denotation* and *connotation* (Mill, 1882), where denotation is thought to concern core semantic meaning, in contrast to any further associations, context, other attributes, and implications that enhance this meaning (connotation). For example, one view holds that the meaning or content of a signal is 'information that has become ritualised and decoupled from the relevant contexts' and thus semantics is borne of pragmatics (Skyrms & Barrett, 2019, p. 37). So, the signal/word 'cat' could refer conventionally to any cat, or 'cat' could refer to a specific cat in the vicinity, whose identity is determined on the basis of pragmatic (or contextual) information.

This distinction between semantics and pragmatics also led to the creation of the term *functional reference* (Macedonia & Evans, 1993; Berthet *et al.*, 2018). This term describes how non-human signals are elicited by a specific class of stimuli that cause adaptive behaviour notably in the absence of context, so that non-human communication may appear to correspond to the referential quality of language(s) but only in a superficial way given the uncertainty over the complexity of non-human communication and active intentionality. Functional reference can be applied to chicken (*Gallus gallus domesticus*) food calls (e.g. Evans & Evans, 1999), or in discussions of vervet monkey (*Chlorocebus pygerythrus*) alarm calls, where each call seems to refer (or at least co-relate) to a specific predator (Seyfarth *et al.*, 1980). However, the value of the term functional reference has been questioned (e.g. Wheeler & Fischer, 2012). Moreover, there are challenges to keeping semantics apart from pragmatics.

Semantics is usually deemed contextless, as with Hockett's *semanticity* (Hockett, 1959; Hockett & Altmann, 1968), one of a set of design features that Hockett argues separates language from (animal) communication. From this perspective it is thought that 'referential signals should be sufficient, in the absence of the eliciting stimulus and of other normally available cues, to allow receivers to select appropriate responses' (Macedonia & Evans, 1993, p. 180). Yet, there are those who argue context is always involved in meaning

and linguistic expressions of that meaning. For instance, reference does not necessitate independence from context: a simple phrase like 'the cat sat on the mat' will relate to a specific cat and a specific mat in a short story, on account of the use of the definite article 'the' rather than the indefinite article 'a' which pertains to the concept of 'cat', where no cat is considered specifically. Therefore, definite contextual as well as indefinite contextless reference exists. Yet, within the non-human literature, the context independence of semantic relations is coalesced into a concept of referentiality for non-human communication, where contextless reference is predominantly studied (e.g. Evans, 1997).

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

To understand the important role of context, and thus pragmatics, consider a word like 'practice'. Its meaning is quite different when applied to a medical student who is learning how to operate, as compared to the work of a professional surgeon, particularly from the view of the patient. Moreover, as Beecher (2021) points out, a non-human signal like those of vervet monkeys may be used to represent different things in different contexts, such as alarm calls or intergroup fights, but the fixed sense and referent link remains within each separate context, just as it does for human words that may be used polysemously (with more than one meaning). For example, the English word 'get' can be used as relating to procuring an item or understanding a concept, as in the phrases 'I will get a drink' or 'I get what you're saying'.

(*b*) *Pragmatics*

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

Scott-Phillips (2015) goes further than others and argues that only pragmatic meaning may be found amongst non-humans because conventionalised semantics evolved out of pragmatic communication and non-humans have not reached the semantics stage. He states that non-humans can determine relationships between the world, actions, and reactions in 'coded communication', if not to the extent of ostensive-inferential communication as found in language. Ostensive-inferential communication involves the expression and recognition of communicative intentions (Grice, 1957; Sperber & Wilson, 1995) that are made possible by *theory of mind* (Premack & Woodruff, 1978), which involves understanding the minds and intentions of others. It is still debated whether theory of mind exists in non-humans [see Krupenye & Call (2019) for a detailed review]. Scott-Phillips (2015) proposes that over the course of human evolution conventional codes developed from this foundation of ostensive-inferential communication. He argues that both pragmatics and analogies to the social-cognitive mechanisms underpinning language should be sought in other species, rather than semantic meanings.

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

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

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)
Humans	**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

Note: Shade indicates the crux between the two approaches.

Again, the occurrence of reference should not be limited to cases where there is a lack of context.

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

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

(3) Information transfer and influencing behaviour

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

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

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

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

However, Dawkins' (1986) point about not using the term *information* can be refuted because whether the information is relevant or redundant for the perceiver does not necessarily affect the informational content of a message or signal. For example, a newspaper whose headline stories are already known to the reader still contains news, just old news as far as that reader is concerned. Meanwhile, alarm calls may be repeated by an individual more than is necessary to alert the group to impending danger, but this does not remove the alarm nature of the call. Moreover, information comes in many forms as seen with longer alarm calls potentially communicating a higher level of immediacy of danger to conspecifics (McLachlan & Magrath, 2020), as well as information about a predator's approach. More interestingly, acoustically similar calls can elicit different responses and *vice versa*; meanwhile other animals can eavesdrop and pick up on the referent of a signal – perhaps danger or a food resource – without the signaller's intent or awareness (Seyfarth *et al.*, 2010). These instances demonstrate that at least some information exists within non-human signals aside from any signaller manipulation. Additionally, Graham & Hobaiter (2023) demonstrated that untrained humans appear to understand common non-human ape gestures. This highlights evolutionary gestural connections and provides a window into the mind of non-humans. So, while Dawkins (1986) may be right to be cautious in assuming human observers can determine information transferred in non-human communication, this does not mean that information transfer does not occur.

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

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

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

is distinguished from other types of influence, precisely because signals benefit signallers *via* the information they transfer to perceivers.

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

(4) Communicative intentionality

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

Grice's (1957) non-natural meaning is more complex, usually relating to symbolic communication in language, and, most importantly, involves intentionality and recognition of that intentionality. Grice focuses on the role of overt intentionality, also known as ostensive inference, which requires mental belief ascription to others (Bar-On & Moore, 2017) and the active influence of others to take note of one's intended meaning. Consequently, this theory proposes that for communicative meaning to arise, a signaller must have a goal and intend to communicate that goal, like feeling thirsty and wanting to let a server at a cafe know this so that one's cup may be refilled. Meanwhile the perceiver – here the server – needs to recognise the goal as well as the signaller's intent to communicate that goal, so that they see the lifted empty cup and recognise that the signaller is trying to get attention to notice the empty cup, for it to be refilled.

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

Some argue that communicative intentionality is very simply a human-only capacity (e.g. Tomasello, 2003), while Rendall *et al.* (2009) argue that non-human signallers fail to account for perceivers' informational needs and so fail to demonstrate perspective taking and theory of mind that can be considered fundamental to language. Others downplay meaning's need for complex cognition including communicative intentionality, proposing intermediary levels that may be found amongst non-humans, as well as pre-verbal infants. For instance, Moore (2018) argues that using eye contact or similar gestures to attract attention to one's signal is frequent and deliberate across species but does not require any reflection, the attributing of communicative intent to a signaller, or inferring mental states to still fulfil the requirements for Gricean non-natural meaning.

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

Meanwhile others argue that certainly intentionality, if not communicative intentionality, is fully present within non-humans, from Veit's (2022) discussion of ways to proceed with comparative study of consciousness to the Cambridge Declaration on Consciousness (2012: https://fcmconference.org/) stating that 'Convergent evidence indicates that non-human animals have the neuroanatomical, neurochemical, and neurophysiological substrates of conscious states along with the capacity to exhibit intentional

behaviours'. In fact, and most importantly for this discussion, one statement made elsewhere about bonobos (*Pan paniscus*) is that 'Because the gestures are intentionally produced, these outcomes are not only the gestures' "functions"—they are their "meanings" (Graham *et al.*, 2018, p. 9; see also Byrne *et al.*, 2017).

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

(5) Multifaceted theories of meaning

Another noticeable trend in the literature, although the importance of this has not been made explicit until now, is that meaning is multifaceted. As mentioned above, Grice (1957) breaks down meaning into two forms: natural and non-natural meaning, where only the latter is deemed important for communication between conscious interactants and can be considered true meaning. However, according to Kalantzis & Cope (2020), five functions can be found in any meaning: reference, agency, structure, context, and interest (expressing purpose). Leech (1974) classifies meaning into seven 'ingredients' with primary importance placed on 'conceptual meaning', which relates to semantics and denotation. Leech's (1974) 'connotative meaning' includes what conceptual meaning refers to, as with Frege's (1948) referents (contrasting with sense). Leech (1974) adds types of associative meaning: 'stylistic meaning' for social use; 'affective meaning' relating to emotions; 'reflected meaning' relating to semantic networks that are conjured mentally when one concept arises; and 'collocative meaning' in terms of linguistic environmental associations. Lastly, Leech (1974) proposes 'thematic meaning', which involves organisation by a signaller in terms of ordering, focus, and emphasis. To Leech (1974), meaning in a wider sense can be termed 'communicative value'. Ogden & Richards (1946, pp. 186–187) compiled a list of over 20 definitions of meaning. These include meaning being described as an intrinsic property, a connotation of a word, an essence, a volition or intended event, practical or theoretical consequences of events or utterances, and that which a user or an interpreter refers to. In sum, the literature pertaining to humans at least, where meaning is not only generally accepted but is also analysed extensively across disciplines, demonstrates that meaning is a complex phenomenon, and it appears to have multiple facets. What is of particular interest is that when the literature across disciplines and species is compared, similar themes emerge that facilitate the development of a comparative framework like the one we develop here.

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

Austin's *locutionary speech acts* refer to utterances *per se*: the surface meaning of the words in the statement or question that involve the sense and referent. So, if you asked someone at dinner 'Is there any salt?' it might be interpreted as if you were wondering about the existence of salt in the world (serving as a possible referent for the word *salt* in this question). *Illocutionary speech acts* refer to the hidden meaning, implication, or layered meanings that co-exist with the surface meaning of the utterance. In this instance, when you ask 'Is there any salt?' a more likely interpretation is that you are asking about the existence of salt in the vicinity of the meal, or one step further, that you are enquiring about the salt's close proximity because you wish to obtain some to add to your meal to enhance its flavour. However, none of that information is actually expressed in the utterance itself. The third *perlocutionary speech acts* relate to the outcome of an interaction. Therefore, once you have asked 'Is there any salt?' and your dinner companion has inferred that you are implying the question 'Is it possible (and acceptable) for me to acquire some salt to put onto my dinner?' your companion may respond in any number of ways. This might include pointing to where the salt is kept, ignoring your question altogether, or cooperatively fetching the salt and placing it next to your plate. An interpretation of non-human communication based on speech act theory could be a growl from a dog in a play context. The surface meaning of the growl is an aggressive threat display to warn another animal to stay away. However, the hidden meaning, that the growl is only an empty gesture, may be revealed by the dog's concurrent provision of a toy, which will encourage perceivers to interpret the growl as a play signal instead of an aggressive signal. As a result, the perceiver may be encouraged to engage in playful activity with the dog.

Therefore, Austin's (1975) speech act theory describes how there are different aspects of meaning contained in and around an utterance, or *communicative signal* in more interdisciplinary terminology. However, rather than simply cataloguing different types of meaning, like Ogden & Richards (1946), Austin's (1975) framework presents three clearly defined and distinct functions of communicative signals and ways in which meaning arises. Importantly, meaning does not just have to be carried or encoded by the signal itself, as assumed in traditional semantics or information theory (Shannon & Weaver, 1949), or as Saussure (1966) describes, where meaning is packaged and unpackaged as similarly as possible in the minds of the signaller and perceiver. Rather, as per the term coined by Grice (1975), there can also be

implicature involved: that is meaning that is not strictly signalled but is hinted at, suggested, and implied. Moreover, it may be argued that meaning is not fully realised until an understanding is achieved on the part of the perceiver, and an outcome of a communicative interaction occurs that coheres in some way with the original signal and/or implicatures, to the benefit of the signaller for adaptive fitness. Austin's (1975) work thus raises the important question of where the meaning arises within a communicative interaction, if it is not a blend of all three aspects: the signal, the intentions and context behind and around the signal, and the outcome(s) of the signal. This also relates to Ongstad's (2021) breakdown of communication into a triad of form, reference, and act.

Essentially, there are very different approaches and foci across disciplines when it comes to the subject of meaning. Overall, one way to differentiate the main variation lies in thinking of meaning either in terms of abstract relations or reference, or in terms of social influence. Within human-centric research, mental representation and the nature of concepts, overt and covert intentions, as well as how these are expressed symbolically form the focus of study, especially given the confidence of such attributes in human cognition. From an evolutionary perspective, the focus remains closely tied to the functional role of meaning, including behavioural influence and the fitness benefits acquired from communication, which has led to discussions of information transfer *versus* behavioural manipulation as the main purpose of communication. This is not tantamount to suggesting that meaning is a different phenomenon depending upon discipline or indeed species. Rather, the apparent distinctions may come down simply to the fact that we struggle to measure mental representation and abstract relations in non-humans, and this limits our focus to their behaviour.

Having broadly explored the key themes and terminology relating to meaning across disciplines and species, it is clear that there is complexity, nuance, and variation in how meaning is discussed. More importantly, it becomes clear that meaning has multiple facets to it and that it is (at least partly) contextually dependent. Austin's (1975) tripartite analysis of speech acts, as detailed above, aligns most closely to the various discussions of meaning across disciplines and species, although this was never the original intent of Austin's work.

One overall point, which particularly stands out, is that most of the literature does not actually question or attempt to define the concept of meaning itself. Instead, different fields have focused on different facets of meaning: from how and where it is encoded, to the signaller and perceiver's possible roles in how meaning arises, to what possible outcomes derive from communicative interactions, and how they align with the goals of the signaller and/or perceiver. In short, we are discussing one phenomenon with different facets. There are not many different types or definitions of meaning, but rather there are numerous 'ingredients' of meaning to use Leech's (1974) term.

III. A MULTIFACETED MEANING FRAMEWORK

(1) A multifaceted framework

Given the cross-disciplinary review in Section II, there seems to be strong agreement across disciplines that whatever meaning is, it is an important aspect of communication (e.g. Austin, 1975; Grice, 1975; Higham & Hebets, 2013). It involves conceptual representation, as well as expression in a communicative setting (e.g. Evans, 2016; Fitch, 2019). It involves some degree of goal-directedness, if not full (communicative) intentionality (e.g. Grice, 1957; Halliday, 1975; Moore, 2018). It requires a response on the part of the perceiver (e.g. Rendall *et al.*, 2009; Ruxton & Schaefer, 2011). Additionally, the outcomes of a communicative interaction must be consistent with the signaller's goals and/or intentions, often referred to as functional or fitness benefits in the non-human literature (e.g. Artiga *et al.*, 2020; Grice, 1957; Ongstad, 2021). Different disciplines concentrate on different aspects or facets of meaning largely through tradition or necessity, while meaning itself is multifaceted but still represents one phenomenon that arises within communication.

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

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

As Table 1 illustrates, Austin's (1975) framework is a productive way to integrate discussions about meaning in communication for both humans and non-humans because it includes surface meaning, implied meaning, and meaning outcomes. This provides a useful basis for the three meaning facets we will describe, alongside their related topics and discussions, such as reference, intentionality, and fitness benefits. In fact, all three meaning facets, associated with signals, interactants, and action outcomes, occur in just one sentence in an article on non-human behaviour: 'the calls and gestures the animals produce, the attention they show to one another, the extent to which one animal's actions 'fit' with another's, etc. – are all familiar aspects of what we typically think of as animal communication' [Johnson, 2015, p. 231 (emphasis added)]. The rest of this section describes

how Austin's (1975) theory motivates and creates a foundation for our theoretical framework of meaning. Following this, we discuss each of the three proposed meaning facets in more detail.

(2) Austin's speech acts as a basis to understand meaning

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

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

In both speech act comparisons, non-human communication and any meaning it may involve have been studied in how they relate to language. However, non-human communication and any potential associated meaning are studied in behavioural terms too. This is captured best in relation to Austin's (1975) perlocutionary speech acts, or outcomes of a communicative interaction, as well as two of Tinbergen's (1963) principles for studying animal behaviour: ontogeny and evolutionary history, given the proximal response and benefit(s), or *function(s)*, as well as longer-term adaptive value(s) of successful communication. This situates the current debate about the purpose of non-human communication: is it used for information transfer or to manipulate perceiver behaviour?

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

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

(3) Three facets of meaning

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

To substantiate our own framework further, a recent paper (Watson *et al.*, 2022) has created a framework for studying part of the evolution of arbitrariness in (non-)human communication that mirrors the same type of approach we take herein for the study of meaning. Watson *et al.* (2022) propose five dimensions in their framework involving: signal production, signal adjustment, signal usage, combinatoriality, and signal perception, which partially correlate to our three key facets outlined above. However, Watson *et al.* (2022) avoid discussion of meaning, whereas we focus on this very topic, due to the difficulty of defining meaning and the contentious debate over whether non-human signals involve meaning. Watson *et al.* (2022) opt for more ambivalent 'communicative function' terminology. Similarly, Raviv, Peckre & Boeckx's (2022) explanation of the apparently inverse

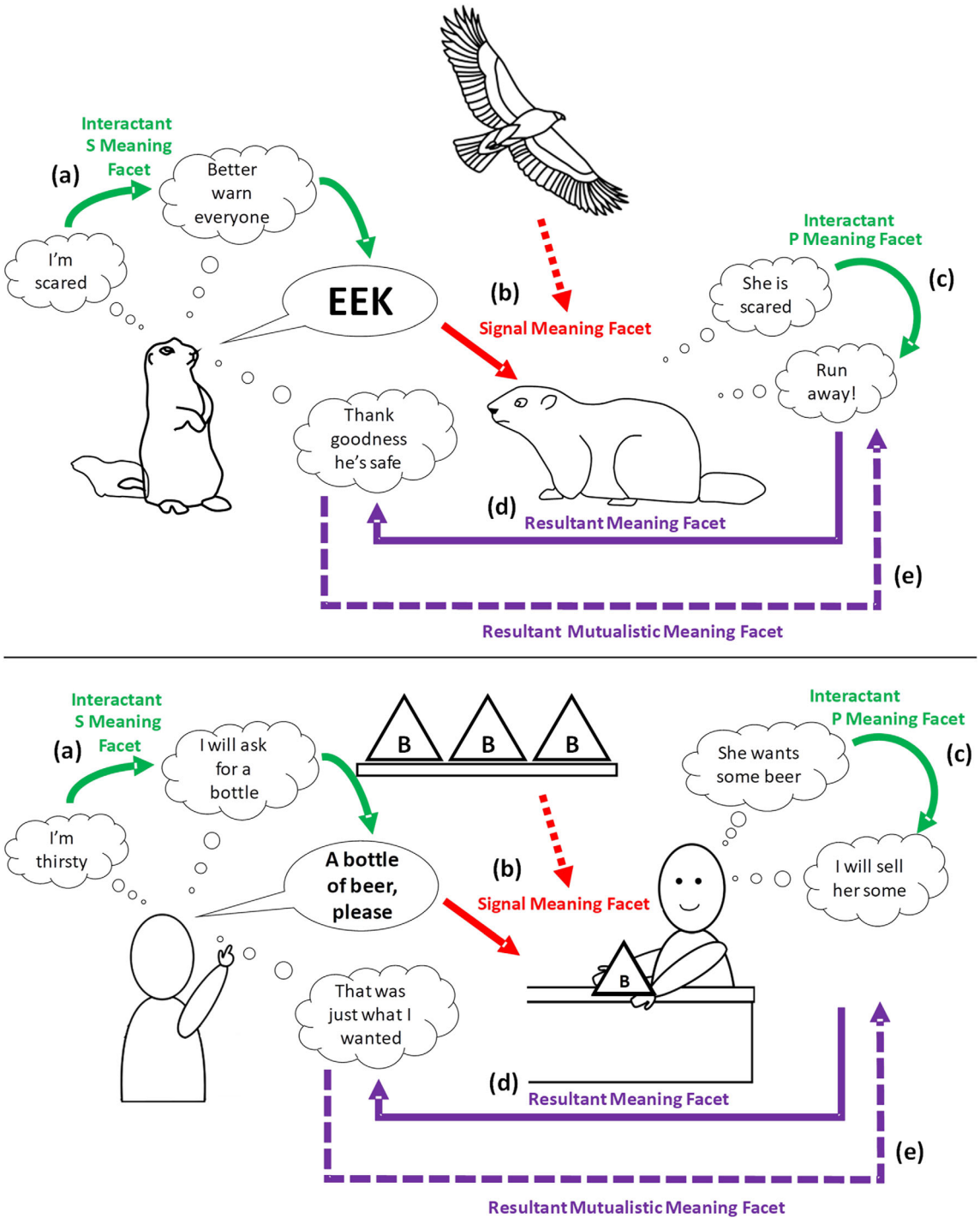

Fig. 1. How meaning arises between individual non-humans (upper) and humans (lower). The figure illustrates how meaning may be understood to arise in human and non-human communication. (a) The signaller's cognitive processes motivate a communicative signal, the *Interactant S Meaning Facet*. (b) This signal occurs *via* a communicative modality (e.g. acoustic), and co-relates (or refers) to an external stimulus (e.g. the eagle), which is part of the *Signal Meaning Facet*. (c) The perceiver interprets the signal and forms a cognitive inference and interpretation, the *Interactant P Meaning Facet*, which may or may not fully – but must partially – correspond to the *Interactant S Meaning Facet*. (d) The behaviour of the perceiver is altered in a way that produces the result desired/evolutionary outcome required by the signaller, which is the *Resultant Meaning Facet*. (e) In the case of mutualistic interactions, there may also be correlation between the goals of the signaller and perceiver, a *Resultant Mutualistic Meaning Facet*, with the roles being reversible, as is common in human dialogue. Here, mutual understanding is frequently signalled from both sides: 'Shall we go for a walk?'–'Yes'–'Good'.

relationship between social complexity and signal variability exhibited across humans and non-humans works on the basis that meaning cannot be inferred for other animals' communication. The authors note that we can only distinguish non-human signal variability based upon the signal's distinctive features, akin to the approach taken to linguistic phoneme (sound form) analysis before the layer of meaning is built in for human communication. At this purely phonemic level, the variability increase, for bigger and more complex societies, is fairly consistent across species. However, when pairing phonemes with their referent, giving the sound signal a layer of meaning, this reduces the levels of possible variability within human communication and establishes more conventionality or arbitrariness. Thus, establishing meaning in non-human communication would lead to a vastly different interpretation of the evidence put forward by Raviv *et al.* (2022).

IV. SIGNAL MEANING FACET

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

(1) The signal and its content

Even the notion of what a signal is has attracted considerable attention. Scott-Phillips *et al.* (2012) state that *communication* involves both a signal and a response behaviour, which are functionally interdependent. Meanwhile, Maynard Smith & Harper (2003) and Higham & Hebets (2013) note that *signals* are traits that have been selected for their communicative function, whereas *cues* have not and are incidental.

One important aspect of the Signal Meaning Facet is the actual content or information of any signal meaning. Semantics as a mode of meaning is thought to involve core concepts: truth, aboutness (related both to reference and intentionality), and topic (subject matter), but only the first two have been treated extensively within human-centric studies (Hawke, 2018). Still, the topic or content of meaning is integral where communication is concerned. It has been clarified that information does not simply relate to objective facts external to the signaller but can also include reference to the signaller's affective (emotional) state or their intentions. One example would be a deceptive communication that contains information that is strictly false but faithfully reflects the signaller's intention. However, what topics may be covered within non-human communication remain somewhat elusive and underexplored, particularly while scholars continue to question the bigger issues, including whether non-humans are capable of meaning at all. We hope this framework will help to end this debate by showing that at least some non-humans are not only capable of meaning but that the facets of meaning can be demonstrated in their communication. Understanding the full extent of meaning in non-human communication is then limited only by methodological constraints, and the level and breadth of data gathered.

Another aspect to consider in terms of a signal's content is the *granularity* or 'cognitive zoom' (Tenbrink, 2020, p. 118; Mann & Hoeschele, 2020) at which the signal provides content. Often non-human signals are categorised quite coarsely, for instance mating calls *versus* food calls or other 'prosaic' categories (Byrne *et al.*, 2017). However, whether this adequately reflects the actual level of detail of content within the signal remains to be seen. Even with humans we can categorise our communication very generically, such as complaint or compliment, or go into depth about the specific nature of what has been discussed, from a compliment generally to a more detailed commendation of a colleague's hard work on a particular project.

(2) Shannon and Weaver model of communication

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

the reason we have adopted the term *perceiver* instead of *receiver* alongside *signaller*.

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

(3) Multimodality

Another aspect of language and communication which should not be ignored for its potential to yield meaning within a signal is multimodality, so the Signal Meaning Facet needs to involve this. Shannon & Weaver (1949) proposed a unimodal transmission by signallers, with meaning encoded in the signal, given their model was based upon telecommunications. Moreover, the vocal–auditory channel continues to be the main modality explored in non-human communication research (e.g. Fishbein *et al.*, 2019). However, meaning does not need to emerge from a single modality, and there is a rich literature on multimodal communication (e.g. Higham & Hebets, 2013). Various modalities offer different transmission distances and levels of permanence, and are detected in diverse ways by species, allowing for close-range private or broadcast communication. Meanwhile, different modalities can also contribute different parts of an overall message from a signaller, such as paralinguistics adding to speech, including one's tone of voice or hand gestures. Another instance would be the courtship display of male wolf spiders (family Lycosidae) (Stafstrom & Hebets, 2013), which wave their ornamented forelegs with an accompanying seismic signal. These multimodal displays yield higher mating frequencies than producing the signals separately, suggesting a proximal meaning is attached to the multimodality.

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

(4) Gestalt principle

An alternative view to the formalist compositional approach to meaning structure holds that not everything can simply be the sum of its parts, as with idioms like 'kicked the bucket' which is used to refer to someone dying rather than literally kicking a bucket. This approach is known as the gestalt principle, part of a movement in psychology (Evans, 2007; Lakoff, 1987), and it applies as much to grammar as to the lexicon (vocabulary), like compositionality. The gestalt principle can be seen in the various Construction Grammar theories that have been proposed (e.g. Goldberg, 2019), which propose that learned form–meaning pairings are the building blocks of language, and also by Blending Theory (Fauconnier & Turner, 1996), in which not only new meanings but also new linguistic structures can emerge from the combination of linguistic units that are above and beyond a simple addition of individual parts. This yields amusing compound nouns like 'bookworm' and unusual phrases like 'I sneezed the napkin off the table', where a more traditional grammatical sentence might phrase this as 'I sneezed and the napkin blew off the table'. Arnold & Zuberbühler (2012) touch on gestalt when discussing an alarm call sequence used by putty-nosed monkeys (*Cercopithecus nictitans*) that the researchers refer to as 'idiomatic expressions'. Of the calls that these monkeys produce, their 'pyow–hack' sequences concatenate their separate 'pyow' or 'hack' calls which convey a different meaning entirely. The 'pyow' and 'hack' and various 'hack–pyow' sequences refer to external events, such as specific predator types, and elicit responses including vigilance. Yet, short 'pyow–hack' sequences elicit the group's travel, and the researchers liken this to human idiomatic expressions like 'kick the bucket', where the meaning is not simply derived from its parts. However, this is not the 'syntactic dead end' (Arnold & Zuberbühler, 2012, p. 308) that the researchers suggest. Instead, the gestalt principle supports the idea that 'pyow–hack' sequences are an example of a very language-like instance of animal communication. Moreover, the researchers point out that 'idiomatic expressions' enable signallers to increase the number of messages that can be conveyed by the small repertoire.

Another intriguing example where the gestalt principle might occur within non-human communication is seen in dwarf mongoose (*Helogale parvula*) alarm calls (Collier *et al.*, 2020). This species produces at least three meaningful alarm calls: one for aerial predators, one for terrestrial threats, and a T_3 call which seems to comprise the two other alarm calls that functions as a general alarm to threats. The researchers explore the interpretation of the call's structural analysis, but a gestalt interpretation may be adopted here. The researchers describe the T_3 call as 'a stand-alone, holistically meaningful

call' (Collier *et al.*, 2020, p. 6), which, provided the unit order remains the same in every T_3 call, seems similar to a human idiom, and this interpretation therefore fits the gestalt principle. This is supported because the two subunits of the call are actually two separate mongoose alarm calls: one for aerial predators, the other for terrestrial predators. The meaning of the T_3 call appears, however, to be a general threat, because of the behaviour of the mongooses: the 'absence of differences in reaction strength to T_3 and aerial or terrestrial calls' (Collier *et al.*, 2020, p. 4). Thus, the call might act as a category label referring to threats in general, including ones that are not so easily distinguished into terrestrial or aerial predators, perhaps in the way that we might shout 'Danger!' as opposed to the more specific 'Fire!' or 'Gun!'

(5) Discrete and graded signals

A further point to address when considering ways in which meaning is associated with a signal is the discrete and graded nature of signals: whether signals are distinct or continuous, like alarm calls that differentiate between predator types as opposed to signals relating to more graded emotional expressions (Larter, 2022). In non-humans, graded signals are alleged to be most common (e.g. Studdert-Kennedy, 2005), and discrete signals are thought to be rare potential indicators of referential meaning. However, is this rarity because there is a difference in how we (are able to) transcribe non-human communication and languages, and the lack of a non-human International Phonetic Alphabet equivalent? Or is this based on whether the communication can be categorised as meaningfully discrete for the species using the communication (Kershenbaum *et al.*, 2016), like the compositional account of semantics outlined above? In any case, compositionality is not the sole way in which meaning can be constructed. Although language is typically associated with discrete signals encoding specific meaning, graded forms and flexible meaning patterns do exist (Taylor, 1995, 2019). For instance, grammaticalisation is frequent, in which words change their syntactic function (sentence use) over time (e.g. Croft, 2003). So, the English phrase 'going to' was once restricted to referring to actual motion towards a target location, e.g. 'I am going to Dublin', but has evolved to also refer to intended future actions, as in the statement 'I am going to finish reading this article'. All linguistic categories need to be continuous to a degree, due to the gradually occurring diachronic changes to language (Bybee, 2007). The song of male humpback whales (*Megaptera novaeangliae*) changes over time too, mostly with small transitions, as it spreads across populations from west to east (Garland *et al.*, 2011), which might involve a non-human parallel with grammaticalisation, or at least diachronic sound change, which could have meaning implications. Meanwhile, modal expressions like 'should' have graded meaning (Lassiter, 2020), from a weak suggestion from a friend 'You should try reading this book' to a much stronger statement on a UK government website relating to travel rules during the Covid-19 pandemic 'This vaccination proof should be provided'.

(6) Dynamic signalling

A final factor to consider in terms of meaning encoding for the Signal Meaning Facet is whether we conceptualise meaning as a reification (an almost tangible entity), or as a dynamic cognitive process. Is meaning a static phenomenon that we simply need to find the criteria for and can then compare communication systems against to determine if they do incorporate meaning? Or is meaning an online construction (built by the brain in the moment), for instance as a result of interactant cognition and in relation to changing situations? One reason for this consideration is Croft's (2011) discussion of language as a process rather than a static phenomenon, given its general cognitive basis and that the nature of cognition is inherently dynamic. Due to the close relationship between language and meaning, such an approach may be adopted by analogy to meaning. Croft's argument is used here in addition to Skyrms' (2010) point that signalling structures are not closed fixed interactions but are open and adaptable across species, and they involve a process of cooperative coordination between signallers and perceivers. This is in addition to the many other aspects that are involved in meaning-making, from mental representation to the role of the communicative interactants themselves.

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

V. INTERACTANT MEANING FACET

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

active turn-taking (e.g. Pika *et al.*, 2018). In such systems like turn-taking, involving flexibility, timing, and various responses, which are increasingly being studied comparatively (Heesen *et al.*, 2022), we can see how interactive, collaborative communicative meaning seems to arise in another species and thus illustrates this meaning facet.

(1) Importance of communicative collaboration

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

Planer & Godfrey-Smith (2021) show how meta-semantic traditions fall into two categories: an expressive tradition where meaning is thought of as concepts that signallers are trying to convey or behaviour they are trying to influence, and an interpretative tradition where meaning is based on perceivers' interpretation of signals. Thus, both production and perception must be considered. Indeed, as Steinert-Threlkeld, Schlenker & Chemla (2021) note, there is symmetry between the signal causation and the resultant action, which is why Macedonia & Evans (1993) include both a production and a perception criterion in their functional reference definition. Seyfarth & Cheney (2003), on the other hand, do not incorporate such collaboration in their model, focusing instead on there being simply calls in response to stimuli and, separately, a perceiver extracting information, as more aligned with the notion of *cues* rather than active *signals*. They note: 'Although listeners acquire rich information from a caller's vocalisation, callers do not, in the human sense, intend to provide it. Listeners acquire information as an inadvertent consequence of signaler behaviour' (Seyfarth & Cheney, 2003, p. 33). This, however, does not appear to be the case for grouper fish (*Plectropomus pessuliferus marisrubri*) and coral trout (*Plectropomus leopardus*) that regularly point out prey hiding in crevices to other local predators with distinct vertical headshakes, and even a horizontal 'shimmy' to recruit these other predators to hunt (Vail, Manica & Bshary, 2013).

(2) Interactant S and P meaning facets

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

The Interactant P Meaning Facet involves interactant asymmetries for those who argue that the onus lies with the perceiver to extract information, as well as inferences about signaller intentions and specific content (Bar-On & Moore, 2017). We can also discuss the role of mental representation and how this contributes to meaning, both in terms of de Saussure's (1966) point that meaning resides in the minds of speakers and hearers, and in terms of what perceivers add to meaning construction. For instance, Smith (1977, 1997) distinguishes *messages*, with information encoded by a signaller, from *meaning* as the information a perceiver derives from a signal along with context. Another example is within interactive conversational repair that occurs where meaning temporarily breaks down for humans (Dingemanse, Blythe & Dirksmeyer, 2018). Such repair occurs through, for example, using question words like 'What?' or interjections like 'Huh?'

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

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

VI. RESULTANT MEANING FACET

Finally, the Resultant Meaning Facet focuses on the outcomes of a communicative situation. This facet of meaning

loosely relates to Austin's (1975) perlocutionary speech acts. So, within interactions, one person can make a statement that implies action for another person and the perceiver can either acknowledge the meaning of the statement, corresponding to successful information transfer, or acknowledge their need to adapt their behaviour, corresponding to behavioural influence. In both cases, uptake of meaning and acknowledgment are key to the success of the communication, referred to here as *outcomes*. This facet is especially important for studying non-humans, because our window into their minds is limited, although their behaviour and communicative outcomes are readily apparent. Even so, the salient point made by citing Austin is that this facet pertains just as much to human interactions, even if it is not so commonly studied.

The Resultant Meaning Facet focuses on the benefits or meaning uses for the communicative interactants, especially but not limited to the signaller. From a functional and evolutionary standpoint, as per Tinbergen (1963), a signal can only be adaptive and thus passed on across generations if it accrues benefits for the signaller by maximising (inclusive) fitness. A non-human example might be an automatic, reactive, and affective growl that warns away other animals from stealing food. Any deceptive signal would also belong to this category. It is necessary for signallers to benefit from producing signals, otherwise the signals would not increase fitness and might be eliminated by selection. Perceivers do not need to benefit from signals in the same way, although on balance it may be that perceivers do also benefit in a majority of cases, which would help support the longevity of particular signals. This discussion creates two subdivisions of this meaning facet: a *Resultant Meaning Facet* (d in Fig. 1) for signaller benefit only and a *Resultant Mutualistic Meaning Facet* (e in Fig. 1) where both interactants benefit from the signal.

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

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

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

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

Where there is mutualistic (cooperative) communication, perceivers may also benefit simultaneously with signallers. A non-human play signal can invite a conspecific to engage in joviality and practice sparring, which involves real-time benefit for both parties. Human–wildlife mutualisms form another example, like the honeyguide bird (*Indicator indicator*) leading humans to beehives to share the spoils (Spottiswoode, Begg & Begg, 2016). Sometimes the benefits can be delayed to one or both parties, as with altruistic behaviour. Helping a vulnerable party that is not kin, especially if they are of another species (e.g. dolphins saving floundering human swimmers; Gregg, 2013), can seem like a waste of precious resources. However, altruism can lead to reciprocal altruism (e.g. rats aiding other begging conspecifics, whose actions are

then reciprocated; Paulsson & Taborsky, 2021), cooperative problem solving or hunting, or kin benefits. This can therefore increase an individual's lifespan or create greater environmental 'harmony' which may benefit all involved.

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

Furthermore, the above outcome examples avoided linguistic examples, to ensure that there is no conceptual conflation with semantics that would be involved in the Signal Meaning Facet, while specific mention of intentionality has also been avoided to highlight the distinction from the earlier Interactant Meaning Facet. Although these aspects are all very common across communication systems, the important point to note is that the three facets are separate from one another. The facets can easily be combined, and a clear example would be someone telling their romantic partner, 'I love you', which involves semantic and pragmatic reference, a specific context, intentional overt meaning implications, affective communication, and behavioural influence on a perceiver that (hopefully) benefits both parties. Yet, the three meaning facets must be differentiated similarly to the way that Austin (1975) separated denotation from connotation and outcomes within his speech act theory. This differentiation permits the systematic investigation of each meaning facet across species, even where some aspects of each of the facets remain in dispute, as well as giving clarity over which facet of meaning is being discussed at any one time.

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

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

VIII. LESSONS FROM NON-HUMAN COGNITION AND LINGUISTICS

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

the cognitive capacity for meaning, so that past limited assumptions about non-human communication need not be upheld.

Moreover, the analysis of meaning in Sections II–VI has been important, not just to substantiate and make explicit the importance of the growing tendency in the literature to acknowledge that meaning is a complex multifaceted concept, but also to demonstrate how non-human communication exhibits each of meaning's three different facets, at least to a degree, among some species. However, this very point – that non-humans exhibit these facets – begs the question: why do we still question meaning in non-human communication? Whether or not we can only apply the term *meaning* to communication that exhibits all three facets simultaneously, clearly multiple species are involved in at least one meaning facet discussion and at least some species exhibit all three meaning facets. This is based simply on what science has discovered so far about both non-human communication and about the facets of meaning. We therefore suggest revisiting the term *non-human/animal communication*, which subsumes hundreds of thousands of diverse species, and obscures any understanding of the variations among them. With all these approaches in mind, furthermore, we have shown that the multifaceted approach establishes the presence of at least aspects of meaning in non-human communication. By doing so, we have progressed beyond Kershenbaum *et al.*'s (2016) observation of the lack of agreement over the nature of meaning and the disconnect between theories of human semantics and animal communication because our framework can be applied consistently across all species.

IX. CONCLUSIONS

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

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

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

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

(5) Applying a multifaceted approach to non-human communication research can inform and resolve key debates in the field because non-human communication data sets are growing rapidly with improved equipment, automated recording, and new quantitative approaches for data analysis. It is important that researchers can leverage these data with an integrated approach, so that non-human communication evidence may be interpreted more comprehensively and be compared to language(s) more effectively. Functionalist perspectives that emphasise the role of meaning within language can benefit from this framework too, because it is essential to understand the origin and nature of meaning for how it impacts on an understanding of the evolution and nature of language and communication, the study of all of which will from now on need to involve non-humans more centrally.

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

X. ACKNOWLEDGEMENTS

For Darwin – cherished canine companion, who meant a great deal. This research did not receive any specific grant from funding agencies in the public, commercial, or

not-for-profit sectors. The authors declare that there are no conflicts of interests.

XI. REFERENCES

Adams, F. & Beighley, S. M. (2013). Information, meaning and animal communication. In *Animal Communication Theory: Information and Influence* (ed. U. E. Stegmann), pp. 399–420. Cambridge University Press, Cambridge.

Akçay, C., Tom, M. E., Campbell, S. E. & Beecher, M. D. (2013). Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20122517.

Amphaeris, J., Shannon, G. & Tenbrink, T. (2021). Cognitive linguistics support for the evolution of language from animal cognition. In *Proceedings of the 43rd Annual Conference of the Cognitive Science Society* (eds T. Fitch, C. Lamm, H. Leder and K. Tebmar-Raible), pp. 2609–2615. Cognitive Science Society, Seattle, WA. Electronic file available at https://escholarship.org/uc/cognitivesciencesociety/43/43 Accessed 03.11.2022.

Amphaeris, J., Shannon, G. & Tenbrink, T. (2022). Overlap not gap: understanding the relationship between animal communication and language with prototype theory. *Lingua* **272**, 103332.

Anderson, S. R. (2017). The place of human language in the animal world. In *Formal Models in the Study of Language: Applications in Interdisciplinary Contexts* (eds J. Blochowiak, C. Griscot, S. Durrleman and C. Laenzlinger), pp. 339–351. Springer, Cham.

Arnold, K. & Zuberbühler, K. (2012). Call combinations in monkeys: compositional or idiomatic expressions? *Brain and Language* **120**, 303–309.

Artiga, M., Birch, J. & Martínez, M. (2020). The meaning of biological signals. *Studies in History and Philosophy of Biological and Biomedical Sciences* **84**, 101348.

Austin, J. L. (1975). *How to Do Things with Words*. Clarendon Press, Oxford.

Bar-On, D. & Moore, R. (2017). Pragmatic interpretation and Signaler-receiver asymmetries in animal communication. In *The Routledge Handbook of Philosophy of Animal Minds* (eds K. Andrews and J. Beck), pp. 291–300. Routledge, Abingdon.

Bateson, G. (1966). Problems in cetacean and other mammalian communication. In *Whales, Dolphins, and Porpoises* (ed. K. S. Norris), pp. 569–578. University of California Press, California.

Beecher, M. D. (2021). Why are no animal communication systems simple languages? *Frontiers in Psychology* **12**, 602635.

Berthet, M., Coye, C., Dezecache, G. & Kuhn, J. (2023). Animal linguistics: a primer. *Biological Reviews* **98**, 81–93.

Berthet, M., Neumann, C., Mesbahi, G., Cäsar, C. & Zuberbühler, K. (2018). Contextual encoding in titi monkey alarm call sequences. *Behavioral Ecology and Sociobiology* **72**, 8.

Bickerton, D. (1990). *Language and Species*. University of Chicago Press, Chicago.

Bolhuis, J. J., Beckers, G. J. L., Huybregts, M. A. C., Berwick, R. C. & Everaert, M. B. H. (2018). Meaningful syntactic structure in songbird vocalizations? *PLoS Biology* **16**, e2005157.

Breed, M. D. & Moore, J. (2016). *Animal Behavior*, Second Edition. Academic Press, Elsevier, Oxford.

Brown, G. & Yule, G. (1983). *Discourse Analysis*. Cambridge University Press, Cambridge.

Buller, D. B. & Burgoon, J. K. (1996). Interpersonal deception theory. *Communication Theory* **6**, 203–242.

Bybee, J. (2007). Diachronic linguistics. In *The Oxford Handbook of Cognitive Linguistics* (eds D. Geeraerts and H. Cuyckens), pp. 945–987. Oxford University Press, Oxford.

Byrne, R. W., Cartmill, E., Genty, E., Graham, K. E., Hobaiter, C. & Tanner, J. (2017). Great ape gestures: intentional communication with a rich set of innate signals. *Animal Cognition* **20**, 755–769.

Byrne, R. W. & Whiten, A. (eds) (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford University Press, Oxford.

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. MIT Press, Cambridge.

Clark, H. H. (1996). *Using Language*. Cambridge University Press, Cambridge.

Clay, Z., Smith, C. L. & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: what do these calls really mean? *Animal Behaviour* **83**, 323–330.

Clayton, N. & Wilkins, C. (2017). Memory, mental time travel and The Moustachio Quartet. *Interface Focus* **7**, 20160112.

Collier, K., Radford, A. N., Stoll, S., Watson, S. K., Manser, M. B., Bickel, B. & Townsend, S. W. (2020). Dwarf mongoose alarm calls: investigating a complex non-human animal call. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20192514.

Courtland, S. D. (2015). Detecting animal deception. *The Journal of Mind and Behavior* **36**, 121–138.

Croft, W. (2003). *Typology and Universals*, Second Edition. Cambridge University Press, Cambridge.

Croft, W. (2011). Language as a process. In *Experience, Variation and Generalization: Learning a First Language* (eds I. Arnon and E. V. Clark), pp. 241–260. John Benjamins, Amsterdam.

Dąbrowska, E. (2016). Cognitive Linguistics' seven deadly sins. *Cognitive Linguistics* **27**, 479–491.

Dawkins, M. S. (1986). *Unravelling Animal Behaviour*. Longman, Essex.

Daylight, R. (2017). Saussure and the model of communication. *Semiotica* **217**, 173–194.

de Saussure, F. (1966). In *Course in General Linguistics*, Third Edition (eds C. Bally, A. Sechehaye and W. Baskin). McGraw-Hill Paperbacks, New York.

Deacon, T. (1997). *The Symbolic Species: The co-Evolution of Language and the Human Brain*. The Penguin Press, London.

Demartsev, V., Kershenbaum, A., Ilany, A., Barocas, A., Bar Ziv, E., Koren, L. & Geffen, E. (2014). Male hyraxes increase song complexity and duration in the presence of alert individuals. *Behavioral Ecology* **25**, 1451–1458.

Deuchar, M. (1996). Spoken language and sign language. In *Handbook of Human Symbolic Evolution* (eds A. Lock and C. R. Peters), pp. 553–570. Clarendon Press, Oxford.

Devitt, M. (2021). Semantic polysemy and psycholinguistics. *Mind and Language* **36**, 134–157.

Dingemanse, M., Blythe, J. & Dirksmeyer, T. (2018). Formats for other-initiation of repair across languages: an exercise in pragmatic typology. In *Linguistic Typology: Critical Concepts in Linguistics* (Volume **4**, ed. I. A. Nikolaeva), pp. 322–357. Routledge, Abingdon.

Engesser, S. & Townsend, S. W. (2019). Combinatoriality in the vocal systems of nonhuman animals. *WIREs Cognitive Science* **10**, e1493.

Evans, C. S. (1997). Referential signals. In *Communication. Perspectives in Ethology* (Volume **12**, eds D. H. Owings, M. D. Beecher and N. S. Thompson), pp. 99–143. Springer, Boston.

Evans, C. S. & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behaviour* **58**, 307–319.

Evans, V. (2007). *A Glossary of Cognitive Linguistics*. Edinburgh University Press, Edinburgh.

Evans, V. (2015). *The Crucible of Language: How Language and Mind Create Meaning*. Cambridge University Press, Cambridge.

Evans, V. (2016). Design features for linguistically-mediated meaning construction: the relative roles of the linguistic and conceptual systems in subserving the ideational function of language. *Frontiers in Psychology* **7**, 156.

Evans, V. & Green, M. (2005). *Cognitive Linguistics: An Introduction*. Edinburgh University Press, Edinburgh.

Fauconnier, G. & Turner, M. (1996). Blending as a central process of grammar. In *Conceptual Structure, Discourse and Language* (ed. A. Goldberg), pp. 113–130. Center for the Study of Language and Information, Stanford.

Ferrer-i-Cancho, R. & Solé, R. V. (2003). Least effort and the origins of scaling in human language. *Proceedings of the National Academy of Sciences* **100**, 788–791.

Fillmore, C. J. (1976). Frame semantics and the nature of language. *Annals of the New York Academy of Sciences* **280**, 20–32.

Firth, J. R. (1957). *Papers in Linguistics 1934–1951*. Oxford University Press, London.

Fischer, J. & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience & Biobehavioral Reviews* **82**, 22–31.

Fishbein, A. R., Fritz, J. B., Idsardi, W. J. & Wilkinson, G. S. (2019). What can animal communication teach us about human language? *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20190042.

Fitch, W. T. (2019). Animal cognition and the evolution of human language: why we cannot focus solely on communication. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20190046.

Flower, T., Gribble, P. M. & Ridley, A. R. (2014). Deception by flexible alarm mimicry in an African bird. *Science* **344**, 513–516.

Font, E. & Carazo, P. (2010). Animals in translation: why there is meaning (but probably no message) in animal communication. *Animal Behaviour* **80**, e1–e6.

Frege, G. (1948). Sense and reference. *The Philosophical Review* **57**, 209–230.

Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., Poole, M. M., Robbins, J. & Noad, M. J. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology* **21**, 687–691.

Geipel, I., Kernan, C. E., Litterer, A. S., Carter, G. G., Page, R. A. & ter Hofstede, H. M. (2020). Predation risks of signalling and searching: bats prefer moving katydids. *Biology Letters* **16**, 20190837.

Glock, H.-J. (2012). What is a theory of meaning? Just when you thought conceptual analysis was dead. *Cahiers Ferdinand de Saussure* **65**, 51–79.

Godfrey-Smith, P. (2020). In the beginning there was information? *Studies in History and Philosophy of Biological and Biomedical Sciences* **80**, 101239.

Goldberg, A. E. (2019). *Explain me this: Creativity, Competition and the Partial Productivity of Constructions*. Princeton University Press, Woodstock.

Graham, K. E. & Hobaiter, C. (2023). Towards a great ape dictionary: inexperienced humans understand common nonhuman ape gestures. *PLoS Biology* **21**, e3001939.

Graham, K. E., Hobaiter, C., Ounsley, J., Furuichi, T. & Byrne, R. W. (2018). Bonobo and chimpanzee gestures overlap extensively in meaning. *PLoS Biology* **16**, e2004825.

Greenwald, M. L. (2018). Wernicke's aphasia: auditory processing and comprehension. In *The Oxford Handbook of Aphasia and Language Disorders* (eds A. M. Raymer and L. J. Gonzalez Rothi), pp. 49–74. Oxford University Press, Oxford.

Gregg, J. (2013). *Are Dolphins Really Smart? The mammal behind the myth*. Oxford University Press, Oxford.

Grice, H. P. (1957). Meaning. *The Philosophical Review* **66**, 377–388.

Grice, H. P. (1975). Logic and conversation. In *Syntax and Semantics. Vol. 3, Speech Acts* (eds P. Cole and J. L. Morgan), pp. 41–58. Academic Press, London.

Gutzmann, D. (2020). Semantics vs pragmatics. In *The Wiley Blackwell Companion to Semantics* (eds D. Gutzmann, L. Matthewson, C. Meier, H. Rullman and T. E. Zimmerman). Wiley, Oxford.

Halliday, M. A. K. (1975). *Learning how to Mean: Explorations in the Development of Language*. Edward Arnold, London.

Hare, J. F., Campbell, K. L. & Senkiw, R. W. (2014). Catch the wave: prairie dogs assess neighbours' awareness using contagious displays. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20132153.

Hawke, P. (2018). Theories of aboutness. *Australasian Journal of Philosophy* **96**, 697–723.

Heesen, R., Fröhlich, M., Sievers, C., Woensdregt, M. & Dingemanse, M. (2022). Coordinating social action: a primer for the cross-species investigation of communicative repair. *Philosophical Transactions of the Royal Society B* **377**, 20210110.

Higham, J. P. & Hebets, E. A. (2013). An introduction to multimodal communication. *Behavioral Ecology and Sociobiology* **67**, 1381–1388.

Hobaiter, C. & Byrne, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology* **24**, 1596–1600.

Hobaiter, C., Graham, K. E. & Byrne, R. W. (2022). Are ape gestures like words? Outstanding issues in detecting similarities and differences between human language and ape gesture. *Philosophical Transactions of the Royal Society B* **377**, 20210301.

Hockett, C. F. (1959). Animal 'languages' and human language. *Human Biology* **31**, 32–39.

Hockett, C. F. & Altmann, S. A. (1968). A note on design features. In *Animal Communication: Techniques of Study and Results of Research* (ed. T. A. Sebeok), pp. 61–72. Indiana University Press, London.

House, J. & Kádár, D. Z. (2021). *Cross-Cultural Pragmatics*. Cambridge University Press, Cambridge.

Hurford, J. R. (2007). *The Origins of Meaning: Language in the Light of Evolution*. Oxford University Press, Oxford.

Johnson, C. M. (2015). The cognitive ecology of dolphin social engagement. In *Dolphin Communication and Cognition: Past, Present, and Future* (eds D. L. Herzing and C. M. Johnson), pp. 229–256. MIT Press, Cambridge.

Kalantzis, M. & Cope, B. (2020). *Adding Sense: Context and Interest in a Grammar of Multimodal Meaning*. Cambridge University Press, Cambridge.

Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, Ç., Backus, G., Bee, M. A., Bohn, K., Cao, Y., Carter, G., Cäsar, C., Coen, M., DeRuiter, S. L., Doyle, L., Edelman, S., Ferrer-i-Cancho, R., *et al.* (2016). Acoustic sequences in non-human animals: a tutorial review and prospectus. *Biological Reviews* **91**, 13–52.

Kershenbaum, A., Demartsev, V., Gammon, D. E., Geffen, E., Gustison, M. L., Ilany, A. & Lameira, A. R. (2021). Shannon entropy as a robust estimator of Zipf's law in animal vocal communication repertoires. *Methods in Ecology and Evolution* **12**, 553–564.

Knight, C. (1998). Ritual/speech coevolution: a solution to the problem of deception. In *Approaches to the Evolution of Language* (eds J. R. Hurford, M. Studdert-Kennedy and C. Knight), pp. 68–91. Cambridge University Press, Cambridge.

Krupenye, C. & Call, J. (2019). Theory of mind in animals: current and future directions. *Wiley Interdisciplinary Reviews: Cognitive Science* **10**, e1503.

Lakoff, G. (1987). *Women, Fire, and Dangerous Things: What Categories Reveal about the Mind*. University of Chicago Press, Chicago.

Langacker, R. W. (1987). *Foundations of Cognitive Grammar, Volume 1: Theoretical Prerequisites*. Stanford University Press, Stanford.

Larter, L. C. (2022). Graded signals. In *Encyclopedia of Animal Cognition and Behavior* (eds J. Vonk and T. K. Shackelford), pp. 2995–2999. Springer, Cham.

Lassiter, D. (2020). Graded modality. In *The Wiley Blackwell Companion to Semantics* (eds D. Gutzmann, L. Matthewson, C. Meier, H. Rullman and T. E. Zimmerman). Wiley, Oxford.

Leech, G. (1974). *Semantics*. Penguin, Harmondsworth.

Leth, P. (2021). Utterance interpretation and actual intentions. *Axiomathes* **31**, 279–298.

Lewis, D. K. (1986). *Convention: A Philosophical Study*. Blackwell, Oxford.

Liebal, K. & Oña, L. (2018). Different approaches to meaning in primate gestural and vocal communication. *Frontiers in Psychology* **9**, 478.

Macedonia, J. M. & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology* **93**, 177–197.

Mann, D. C. & Hoeschele, M. (2020). Segmental units in nonhuman animal vocalization as a window into meaning, structure, and the evolution of language. *Animal Behaviour and Cognition* **7**, 151–158.

Martínez, M. (2019). Deception as cooperation. *Studies in History and Philosophy of Biological and Biomedical Sciences* **77**, 101184.

Maynard Smith, J. & Harper, D. (2003). *Animal signals*. Oxford University Press, Oxford.

McLachlan, J. R. & Magrath, R. D. (2020). Speedy revelations: how alarm calls can convey rapid, reliable information about urgent danger. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20192772.

Mill, J. S. (1882). *A System of Logic, Ratiocinative and Inductive, Being a Connected View of the Principles of Evidence, and the Methods of Scientific Investigation*, Eighth Edition. Harper and Brothers, New York.

Moore, R. (2018). Gricean communication, language development, and animal minds. *Philosophy Compass* **13**, e12550.

Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B. & Worm, B. (2011). How many species are there on earth and in the ocean? *PLoS Biology* **9**, e1001127.

Nishida, T. (1987). Local traditions and cultural transmission. In *Primate societies* (eds B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker), pp. 462–474. University of Chicago Press, Chicago.

Ogden, C. K. & Richards, I. A. (1946). *The Meaning of Meaning*, Eighth Edition. Routledge, London.

Ongstad, S. (2021). Can animals refer? Meta-positioning studies of animal semantics. *Biosemiotics* **14**, 433–457.

Owren, M. J., Rendall, D. & Ryan, M. J. (2010). Redefining animal signaling: influence versus information in communication. *Biology and Philosophy* **25**, 755–780.

Paulsson, N. I. & Taborsky, M. (2021). Reaching out for inaccessible food is a potential begging signal in cooperating wild-type Norway rats, *Rattus norvegicus*. *Frontiers in Psychology* **12**, 712333.

Peirce, C. S. (1984). *The Writings of Charles S. Peirce: A Chronological Edition, Volume 2: 1867–1871*. Indiana University Press, Bloomington.

Pepperberg, I. M. (2017). Symbolic communication in nonhuman animals. In *APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior* (eds J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon and T. Zentall), pp. 663–679. American Psychological Association, Washington, DC.

Perniss, P., Thompson, R. L. & Vigliocco, G. (2010). Iconicity as a general property of language: evidence from spoken and signed languages. *Frontiers in Psychology* **1**, 227.

Pietroski, P. M. (2017). Semantic Internalism. In *The Cambridge Companion to Chomsky* (ed. J. McGilvray), pp. 196–216. Cambridge University Press, Cambridge.

Pika, S., Wilkinson, R., Kendrick, K. H. & Vernes, S. C. (2018). Taking turns: bridging the gap between human and animal communication. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20180598.

Planer, R. J. & Godfrey-Smith, P. (2021). Communication and representation understood as sender–receiver coordination. *Mind and Language* **36**, 750–770.

Pleyer, M., Lepic, R. & Hartmann, S. (2022). Compositionality in different modalities: a view from usage-based linguistics. *International Journal of Primatology* 1–33.

Premack, D. & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences* **1**, 515–526.

Raviv, L., Peckre, L. R. & Boeckx, C. (2022). What is simple is actually quite complex: a critical note on terminology in the domain of language and communication. *Journal of Comparative Psychology* **136**, 215–220.

Reboul, A. (2017). *Cognition and Communication in the Evolution of Language*. Oxford University Press, Oxford.

Reddy, M. (1979). The conduit metaphor: a case of frame conflict in our language about language. In *Metaphor and Thought* (ed. A. Ortony), pp. 284–324. Cambridge University Press, Cambridge.

Rendall, D., Owren, M. J. & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour* **78**, 233–240.

Rowell, J., Ellner, S., Reeve, H., Taylor, P. D. & Whitlock, M. C. (2006). Why animals lie: how dishonesty and belief can coexist in a signaling system. *The American Naturalist* **168**, E180–E204.

Ruxton, G. D. & Schaefer, H. M. (2011). Resolving current disagreements and ambiguities in the terminology of animal communication. *Journal of Evolutionary Biology* **24**, 2574–2585.

Scarantino, A. (2013). Animal communication as information-mediated influence. In *Animal Communication Theory: Information and Influence* (ed. U. E. Stegmann), pp. 63–87. Cambridge University Press, Cambridge.

Scarantino, A. (2017). How to do things with emotional expressions: the theory of affective pragmatics. *Psychological Inquiry* **28**, 165–185.

Scarantino, A. & Clay, Z. (2015). Contextually variable signals can be functionally referential. *Animal Behaviour* **100**, e1–e8.

Schlenker, P., Chemla, E. & Zuberbühler, K. (2016). What do monkey calls mean? *Trends in Cognitive Sciences* **20**, 894–904.

Schmid, H.-J. (2020). *The Dynamics of the Linguistic System: Usage, Conventionalization, and Entrenchment*. Oxford University Press, Oxford.

Schweinfurth, M. K., DeTroy, S. E., van Leeuwen, E. J. C., Call, J. & Haun, D. B. M. (2018). Spontaneous social tool use in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **132**, 455–463.
Scott-Phillips, T. C. (2010). The evolution of relevance. *Cognitive Science* **34**, 583–601.
Scott-Phillips, T. C. (2015). Nonhuman primate communication, pragmatics, and the origins of language. *Current Anthropology* **56**, 56–80.
Scott-Phillips, T. C., Blythe, R. A., Gardner, A. & West, S. A. (2012). How do communication systems emerge? *Proceedings of the Royal Society B: Biological Sciences* **279**, 1943–1949.
Seddon, N., Alvarez, A. & Tobias, J. A. (2002). Vocal communication in the pale-winged trumpeter (*Psophia leucoptera*): repertoire, context and functional reference. *Behaviour* **139**, 1331–1359.
Seyfarth, R. M. & Cheney, D. L. (2003). Meaning and emotion in animal vocalizations. *Annals of the New York Academy of Sciences* **1000**, 32–55.
Seyfarth, R. M. & Cheney, D. L. (2017). The origin of meaning in animal signals. *Animal Behaviour* **124**, 339–346.
Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbühler, K. & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour* **80**, 3–8.
Seyfarth, R. M., Cheney, D. L. & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour* **28**, 1070–1094.
Shannon, C. E. & Weaver, W. (1949). *The Mathematical Theory of Communication*. University of Illinois Press, Chicago.
Sievers, C. & Gruber, T. (2020). Can nonhuman primate signals be arbitrarily meaningful like human words? An affective approach. *Animal Behavior and Cognition* **7**, 140–150.
Skyrms, B. (2010). *Signals: Evolution, Learning & Information*. Oxford University Press, Oxford.
Skyrms, B. & Barrett, J. A. (2019). Propositional content in signals. *Studies in History and Philosophy of Biological and Biomedical Sciences* **74**, 34–39.
Smet, A. F. & Byrne, R. W. (2013). African elephants can use human pointing cues to find hidden food. *Current Biology* **23**, 2033–2037.
Smith, W. J. (1977). *The Behavior of Communicating: An Ethological Approach*. Harvard University Press, Cambridge.
Smith, W. J. (1997). The behavior of communicating, after twenty years. In *Communication. Perspectives in Ethology* (Volume **12**, eds D. H. Owings, M. D. Beecher and N. S. Thompson), pp. 7–53. Springer, Boston.
Smith, W. J., Smith, S. L., Devilla, J. G. & Oppenheimer, E. C. (1976). The jump-yip display of the black-tailed prairie dog *Cynomys ludovicianus*. *Animal Behaviour* **24**, 609–621.
Speaks, J. (2021). Theories of meaning. In *The Stanford Encyclopedia of Philosophy (Spring 2021 Edition)* (ed. E. N. Zalta). Stanford University, Stanford, CA. Electronic file available at https://plato.stanford.edu/archives/spr2021/entries/meaning/, Accessed 03.11.2022.
Sperber, D. & Wilson, D. (1995). *Relevance: Communication and Cognition*, Second Edition. Blackwell, Oxford.
Spottiswoode, C. N., Begg, K. S. & Begg, C. M. (2016). Reciprocal signaling in honeyguide-human mutualism. *Science* **353**, 387–389.
Stafstrom, J. A. & Hebets, E. A. (2013). Female mate choice for multimodal courtship and the importance of the signaling background for selection on male ornamentation. *Current Zoology* **59**, 200–209.
Steinert-Threlkeld, S., Schlenker, P. & Chemla, E. (2021). Referential and general calls in primate semantics. *Linguistics and Philosophy* **44**, 1317–1342.
Studdert-Kennedy, M. (2005). How did language go discrete? In *Language Origins: Perspectives on Evolution* (ed. M. Tallerman), pp. 48–67. Oxford University Press, Oxford.
Suzuki, T. N., Wheatcroft, D. & Griesser, M. (2020). The syntax–semantics interface in animal vocal communication. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20180405.
Taylor, J. R. (1995). *Linguistic Categorization: Prototypes in Linguistic Theory*, Second Edition. Clarendon Press, Oxford.
Taylor, J. R. (2019). Prototype effects in grammar. In *Cognitive Linguistics – Key Topics* (eds E. Dąbrowska and D. Divjak), pp. 127–147. De Gruyter, Berlin.
Tenbrink, T. (2020). *Cognitive Discourse Analysis: An Introduction*. Cambridge University Press, Cambridge.
Terkourafi, M. (2021). Pragmatics as an interdisciplinary field. *Journal of Pragmatics* **179**, 77–84.
Tinbergen, N. (1963). On aims and methods of ethology. *Ethology* **20**, 410–433.
Tomasello, M. (2003). *Constructing a Language*. Harvard University Press, London.
Tomasello, M. & Call, J. (2019). Thirty years of great ape gestures. *Animal Cognition* **22**, 461–469.
Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., Goncalves, I. B., Burkart, J. M., Flower, T., Gaunet, F., Glock, H.-J., Gruber, T., Jansen, D. A. W. A. M., Liebal, K., Linke, A., *et al.* (2017). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews* **92**, 1427–1433.
Townsend, S. W. & Manser, M. B. (2013). Functionally referential communication in mammals: the past, present and the future. *Ethology* **119**, 1–11.
Vail, A. L., Manica, A. & Bshary, R. (2013). Referential gestures in fish collaborative hunting. *Nature Communications* **4**, 1765.
Veit, W. (2022). Towards a comparative study of animal consciousness. *Biological Theory* **17**, 292–303.
von Frisch, K. (1967). *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge.
Watson, S. K., Filippi, P., Gasparri, L., Falk, N., Tamer, N., Widmer, P., Manser, M. & Glock, H.-J. (2022). Optionality in animal communication: a novel framework for examining the evolution of arbitrariness. *Biological Reviews* **97**, 2057–2075.
Wheeler, B. C. & Fischer, J. (2012). Functionally referential signals: a promising paradigm whose time has passed. *Evolutionary Anthropology* **21**, 195–205.
Whiten, A. & Byrne, R. (1988). Tactical deception in primates. *Behavioral and Brain Sciences* **11**, 233–244.
Zlatev, J., Steffensen, S. V., Harvey, M. I. & Kimmel, M. (2018). Introduction. *Cognitive Semiotics* **11**, 1–6.
Zuberbühler, K. (2018). Intentional communication in primates. *Revue Tranel* **68**, 69–75.

(*Received 9 November 2022; revised 1 June 2023; accepted 5 June 2023; published online 20 June 2023*)