

Appendix. Formal approaches to animal communication

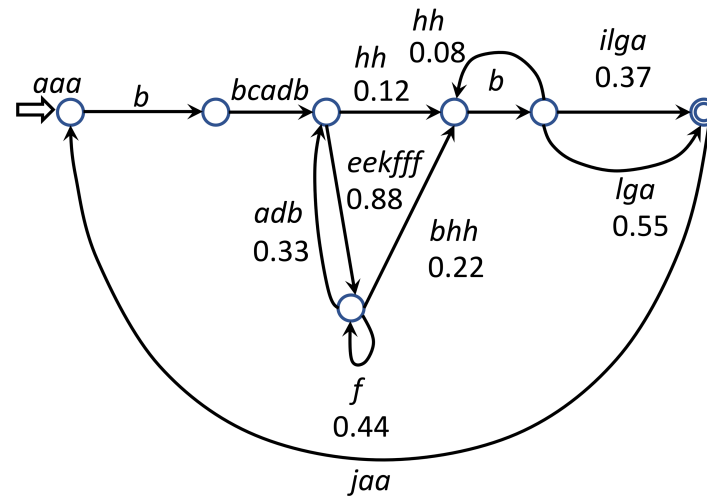
Having outlined the achievements of formal linguistics in connection with the study of human language, we can now turn to its applications to animal communication systems. There are endless debates about appropriate terminology in animal communication, starting with the word 'language': are we justified in applying it to non-human systems, and can we speak of 'animal languages'? Debates about terminology are rarely fruitful, and for good reason in this case: human language is characterized by so many distinct properties that any number of subsets of them could be taken to 'define' language (see Hockett 1959 among many others), while extending differently to other systems. Formal approaches adopt a different method: starting from the notion of 'language' in formal language theory, they treat all sorts of things as languages, namely any system that determines a set of strings as well-formed or not. Once such a definition is adopted, many animal communication systems qualify as languages, and researchers can focus their attention not on the term, but on the properties of these systems with respect to the form of expressions and their meaning.

□ *Animal syntax: the example of birdsongs*

When studying the semantics and pragmatics of animal communication systems, a natural place to start is the calls and gestures of primates, our closest non-human relatives. However, in this empirical domain, little syntactic sophistication has been demonstrated, in that they tend to occur as isolated or juxtaposed units. For an investigation of animal syntax, birds turn out to provide a richer empirical domain.

Here we must start by differentiating bird calls from bird songs. Bird calls, which serve to convey information about the environment (e.g. the presence of predators), have not been shown to have a sophisticated syntax either. But things are different in the area of bird songs, which differ from calls in arguably not conveying information about the environment, and in possibly just advertising the singer's presence and general qualities. It is thus conceivable that birdsongs have a syntax but no clear semantics; and the syntax of bird songs is empirically rich and worth discussing, though it is mostly contained within the bound of Finite State (= regular) languages as discussed in section 2.1.1 (see Berwick et al. 2011). To illustrate, Bengalese finch songs have been analyzed with the finite-state grammar posited in (1) (where states are connected with transition probabilities). Songs are derived from transitioning from one melodic segment to another in a consecutive way. Notably, the type of finite-state grammar shown in (1) is quite sophisticated in that it involves multiple states that can produce diverse strings; it exemplifies that such grammars are found in the animal kingdom.

- (1) Syntax of Bengalese finch song (redrawn from Berwick et al. 2011:117, a slight adaptation of Hosino & Okanoya 2000:2093); the diagram shows probabilistic finite-state transitions; the labels indicate note sequences and transitional probabilities



This leaves three important questions open. First, are there cases in which animal syntax goes beyond the finite-state bound? Second, do the finite-state rules found in animals have anything to do with human language? Fitch (e.g. 2018) proposes a "continuity hypothesis", according to which "humans share the processing capabilities required to deal with regular-level sequential processing, and thus phonology, with other animals, and these shared capabilities are implemented in homologous neural processing algorithms and circuitry" (p. 72); by contrast, human syntax goes beyond the finite-state bound. Third, do the finite-state languages found in animal communication occupy an interesting subpart of the set of finite state languages? Recent research (such as Berwick et al. 2011) has established a 'subregular hierarchy' (a hierarchy among the formal languages within the finite-state bound), and an application to animal syntax of the formal analysis of this subregular hierarchy has already begun (e.g.; strikingly, this is also the case for human phonology, e.g. Heinz and Idsardi 2011).

□ *Animal meanings: the example of monkey communication*

On the meaning front, it is with respect to monkey communication that the most precise formal tools have so far been used. Contemporary primatology has established that some primate calls and gestures are naturally produced in some situations but not in others; monkey alarm calls are produced in response to the presence of a predator (e.g. Zuberbühler 2009), great ape gestures serve purposes such as to solicit grooming from another ape (e.g. Byrne et al. 2017). Focusing on monkey alarm calls, field experiments have shown that the monkeys themselves know the correlation of calls with predation situations and thus derive information from the calls they hear. Under any name ("appropriate" vs. "inappropriate" or "true" vs. "false"), this means that these signals have a semantics – which is unsurprising since they clearly convey information.

Applying the methods of formal semantics to monkey communication has made two contributions: (i) it has clarified the space of possible theories by stating fully explicit analyses about (a) the meaning of elementary calls and (b) the ways they are combined; (ii) it has generated new potential explanations, especially about the division of labor between semantics and pragmatics. Insights regarding the semantics-pragmatics divide have led to the hypothesis that there are 'animal implicatures', cases in which the meaning of a call is enriched by the assumption that it was the most informative call that could be appropriately used. The main results, discussed in the remainder of this appendix, are as follows:

- (2) a. Elementary calls can often be assigned simple and explanatory meanings.
- b. Call combinations can usually be analyzed without structure, by treating each call as a separate utterance reflecting the caller's information as it is produced: concatenation appears to suffice. The *-oo* component of Campbell's monkey calls is so far the only plausible case of morphology with compositional interpretation at the level of what we may dub 'call suffixes'.
- c. Call meaning might be enriched by an animal version of the Informativity Principle, although this hypothesis needs to be tested further.

□ *Call meaning vs. pragmatic enrichment: Campbell's monkeys¹*

A rich example pertaining to the meaning of individual calls is afforded by Campbell's monkeys (see (3)). Male adults have a non-predation-related call, *boom*. The Campbell's monkeys of the Tai Forest (Côte d'Ivoire) use a call *krak* to raise leopard alerts, and *hok* for raptor alerts. Remarkably, they also have suffixed calls: *krak-oo* is used for unspecific alerts (which may include such things as falling trees), and *hok-oo* for non-ground disturbances. The challenge is to assign meanings to *boom*, *krak*, *hok*, and *-oo*. Further complexity is added by the Campbell's call use on Tiwai Island (Sierra Leone), where leopards haven't been seen for decades: the Tai calls are used, but *krak* raises unspecific alerts (same as *krak-oo*), rather than leopard alerts. Should we conclude that call meaning is subject to a kind of dialectal variation, such as *pants* which has the meaning "trousers" in American English, but "underpants" in British English?

We need to be careful, at this point, to differentiate between observed conditions of use (i.e., what we can observe), and underlying core meanings (i.e., lexical entries). The default assumption in primatology is that the meanings of monkey alarm calls are usually innate. Correspondingly, while one may faultlessly speak of variation at the level of observed conditions of use, there are reasons not to assume dialectal variation in the lexical entries.

Correspondingly, Schlenker et al. (2014) propose an analysis with uniform core meanings, but with a crucial use of the Informativity Principle (see (8) in section 2.3.1). The complete analysis is illustrated in (3), where the observable conditions of use are given in (3)a, while the underlying core meanings are given in (3)b. First, as shown in (3)b, the monkeys take *krak* to trigger general alerts, and *hok* to trigger non-ground alerts. Second, in order to analyze the meaning of the suffix *-oo*, Schlenker et al. assume that if a call *R* is *krak* or *hok*, then *R-oo* indicates a weak alert of the R-type. Thus *hok-oo* indicates a weak (*-oo*) non-ground (*hok*) alert.

(3) **Male Campbell's monkey calls**

a. Description

b. Analysis

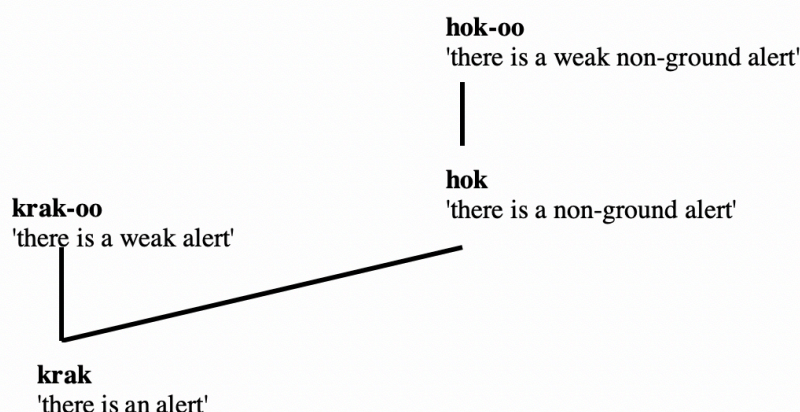
c. Results of call competition

CAMPBELL'S MONKEYS	Call	Typical situations	Literal meanings		Enriched meanings		
	boom boom	non-predation alert	boom boom	non-predation alert	hok	hok-oo	serious non-ground alert
	hok	presence of an eagle	hok	non-ground alert	krak	krak-oo, hok	Tai: alert, serious, ground
	krak	Tai: presence of a leopard	krak	alert			Tiwai: useless enrichment, hence literal meaning only
	hok-oo	Tiwai: unspecific alert	R-oo	weak R-alert			
	krak-oo	hok-oo: alert from above	Informativity Principle				
		krak-oo: unspecific alert	"Prefer more informative expressions!"				

While the core meaning of *krak* (a general alert) is observed in Tiwai island, (3)a, its observable meaning has been 'fine-tuned' to signal the presence of a leopard in Tai forest; to account for this narrowing of *krak*'s meaning in Tai forest, Schlenker et al. employ the Informativity Principle, with the informativity relations in (4): *hok-oo* is more informative than *hok*, *krak-oo* is more informative than *krak*, and, instrumental to the analysis, *hok* ('there is a non-ground alert') is more informative than *krak* ('there is an alert'). We can then show why *hok* 'there is a non-ground alert' is understood to mean 'there is a raptor' in both Tai and Tiwai, and why *krak* 'there is an alert' in Tai is understood to mean 'there is a leopard'.

¹ This section and the next borrow from Schlenker et al. 2016c.

- (4) **Informativity relations among Campbell's calls (for two calls that are linked, 'higher' means 'more informative')**



First, *hok* competes with another call, namely *hok-oo*; *hok-oo* (pertaining to *weak* non-ground alerts rather than to any non-ground alert) is more specific than *hok*, with the effect that the meaning of *hok* is enriched to *hok but not hok-oo*: as a consequence, *hok* only applies to aerial (= *hok*) alerts that are non-weak (= *not hok-oo*) – hence, *hok* is used for raptors.

By the same logic, the unspecific alert *krak* competes with two calls: with *krak-oo*, but also with *hok*. Due to this competition with two more informative calls, *krak* can only be used for *ground* (= *not hok*) *disturbances that are serious* (= *not krak-oo*) – provided that serious ground disturbances exist, for otherwise this pragmatic enrichment would lead to a contradiction. This pragmatically enriched meaning surfaces in the leopard uses of *krak* that are observed in Tai. Crucially, if serious ground disturbances are taken out of the picture, as in Tiwai, where leopards are absent, then pragmatic enrichment fails to apply (for otherwise it would give rise to a contradiction); *krak* collapses into being interchangeable with *krak-oo*, as they no longer differ in informativity and have a completely general meaning. Importantly, while in human language the Informativity Principle is often taken to derive from more general rules of communicative rationality, it might conceivably be hard-wired and automatic in non-human primates.

□ *Call combination vs. context change: Titi monkeys*

The calls of the Titi monkeys of South America make a different point, namely that not everything that looks like a complex syntax/semantics interaction requires complex composition rules. Titi monkey alarm calls also predominantly deal with two raptor types, namely cats² and raptors; much of the literature has focused on two calls, simply labeled *A* and *B*, since they sound like high-pitched squeaks or whistles to a human ear, and thus do not lend themselves to more mnemonic names.³

The initial puzzle is that by re-arranging the *A* and *B* calls in various ways, Titi monkeys can provide information about both *predator type* (cat, raptor) and *predator location* (on the ground, in the canopy). We simplify somewhat, and write X^+ for a series of iterations of call *X* in a sequence. B^+ is used for non-predation alerts and for situations involving a cat on the ground, while $A B^+$ is used in situations that involve a cat in the canopy. A raptor on the ground

² Note that we use the term *cat* in the broad sense ‘felid’ – leopards, jaguars, cougars, etc. –, and not in the narrow sense ‘domestic cat’.

³ See e.g. Căsar (2012:71) and Căsar et al. (2012:406) where the *A*-call is introduced with the descriptive parenthesis ‘chirp’, and the *B*-call with the descriptive parenthesis ‘cheep’.

gives rise to an A^+B^+ sequence, while a raptor in the canopy triggers an A^+ sequence. The main patterns that were observed are summarized in (5)a.

Should we conclude that these sequences have a complex syntax/semantics interface, as suggested by Cäsar et al. 2013? Or should they be treated as very long idioms, with no internal semantics? As we will see, a concatenative approach has been explored (Schlenker et al. 2016a), which treats each A call and B call as a separate utterance appears to be sufficient, coupled once again with a highly minimal core meaning for the two calls, as given in (5)b. As in the case of Campbell's monkeys, the Informativity Principle will then give rise to enriched meanings, (5)c, and we can derive the observable patterns from insights on the nature of how interactions between Titi monkeys and predators typically evolve. Once these pieces are in place, we see that there is no evidence that combinations of monkey alarm calls exhibit syntactic structure, in sharp contrast to bird song.

(5) **Titi monkey calls**

a. Description

b. Analysis

c. Results of call competition

TITI MONKEYS

Call	Typical situations	
B ⁺	non-predation alert	
B ⁺	cat	on the ground
A B ⁺	cat	in the canopy
A ⁺ B ⁺	raptor	on the ground
A ⁺	raptor	in the canopy

Literal meanings

A	serious non-ground alert
B	alert

Informativity Principle
 “Prefer more informative expressions!”

B⁺ correspond to ground or weak alerts
 (or alerts that *have become* weak alerts)

(Raptors in the canopy remain serious threats
 even after having been signaled by As)

Let us start by addressing the core meanings of A calls and B calls; it is most natural to look at the A^+ -sequences (= series of A -calls) and B^+ -sequences first. Since the B -call is used in predatory and non-predatory situations alike, one may take it to trigger an unspecific alert (coded as 'alert' in (5)b). By contrast, in field experiments, the A -call triggers an immediate 'looking up' behavior, a behavior in Titi monkeys associated with scanning the sky for serious arial threats; one can thus posit that an A -call is indicative of a *serious non-ground alert*. These assumptions explain why one finds B^+ -sequences (= series of B -calls) in 'cat on the ground' situations, and A^+ -sequences in 'raptor in the canopy' situations. On the one hand, an A -call wouldn't be used in a situation that is either not serious or involves a ground alert. On the other hand, the Informativity Principle explains why the unspecific B -call, which *could* be used in a 'raptor in the canopy' situation (as it merely means 'alert'), *fails* to be used in such a situation, even though it would be applicable: it would simply be under-informative.

But why does one find A^+B^+ in 'raptor on the ground' situations? A remark about hunting techniques proved suggestive: raptors on the ground usually attack by *flying*, hence the serious non-ground alerts A^+ , as the raptor may at any point rise into the air and then attack. Still, being on the ground isn't a typical hunting position, and if the raptor stays on the ground, the alert stops being serious after a while, which only leaves B as a possibility. The opposite (a sequence of B -calls followed by A -calls) would naturally be inapplicable in a similar situation. In 'cat in the canopy' situations, by contrast, one finds AB^+ sequences, possibly because a serious non-ground danger is indicated with the initial A -call, but this quickly transitions to a weaker danger (thus befitting a B -call) since a cat becomes less dangerous after detection (Zuberbühler et al. 1999).

On this view, which is still the subject of active debates,⁴ the apparent complexity of Titi sequences might reflect the interaction between simple meanings and the evolution of the contextual environment as the sequence unfolds, rather than a complex syntax/semantics interface or very long idioms. Such a view is also supported by functional considerations: Titi call sequences tend to be long and follow a slow time course, which makes it unlikely that they

⁴ Berthet et al. 2019a,b fail to replicate the AB^+ sequences in 'cat in the canopy' situations, finding instead B^+ , with A 's interspersed; they also develop a somewhat different theory.

are interpreted non-compositionally as idioms because hearers would need to wait too long for the meaning of the message to be effective.

In sum, the Campbell's and Titi studies illuminate several points: (i) they clarify the possible core meanings of individual calls; (ii) in the case of Campbell's -oo, they make it plausible that there is a tiny composition rule at the level of a suffix *within* calls such as *krakoo* and *hokoo*; (iii) in both species, there seem to be general alert calls, but their use is constrained by the Informativity Principle; (iv) in all cases, a call can be treated as a separate utterance, and no non-trivial composition rules are needed at this point – and in particular no call-external application of functional application, as in the combination of words in human language syntax.

□ *New questions about the evolution of animal meanings*

The investigation of primate calls has another benefit: in some cases, it yields insights into the evolution of animal meanings. As an example, *booms* are non-predation-related calls present, not just in Campbell's monkeys, but also in many cousin subspecies of the family cercopithecines. Inspection of their distribution strongly indicates that *booms* were present several million years ago in the repertoire of the most recent common ancestor of entire subgroups (Schlenker et al. 2016b). Combined with the primatology view that core meanings of monkey alarm calls are innate, the picture that emerges is that the meanings associated with *booms* might have also evolved at the time of the most recent common ancestor, currently estimated to have lived more than 10 million years ago.

Call evolution raises important questions with regards to what are the constraints on possible calls, in particular the following: under what conditions can the simultaneous presence of specific ('serious non-ground alert') and general ('alert') calls be stable? Steinert-Threlkeld et al. 2021 show that under broad modelling conditions, general calls are unstable: a Titi-style general B-call competing with a specific A-call meaning *serious non-ground alert* should lead in later generations to a division of lexical labor, with the B-call meaning not-A as part of its core meaning, i.e. *non-[serious non-ground] alert*. If so, the Informativity Principle won't have anything to operate on, since call meanings will never be in a specific-to-general relation. To counter this conclusion, we might however surmise that *non-[serious non-ground] alert* is not a possible concept because it does not correspond to a natural class of objects. But showing this requires an independent study of constraints on animal concepts, a point we briefly alluded to in section 6.1.

Turning to ape gestures as another type of primate signal, Byrne et al. 2017 argue that 36 gestures are shared among all great apes (*Pan*, *Gorilla* and *Pongo*), and likely part of an innate repertoire. On the form side, Hobaiter and Byrne 2017 argue that the overlap among the individual species' repertoires, which makes up the shared repertoire, is unlikely to be due to limitations of the articulatory possibilities for gestures. On the meaning side, Graham et al. 2018 argue that partial similarities in gesture use among bonobos and chimpanzees are also unlikely to be due to chance. This suggests that a core set of gestures and gestural meanings is innate and had evolved by the time of the last common ancestor of the great apes, currently estimated to have lived 17 million years ago.

Strikingly, ape gestures are an area in which a genuine connection with human communication might be non-speculative, as argued by Kersken et al. 2018. They uncover a human infant gestural repertoire of which 96% (50 out of 52 gestures) are shared with apes. A further step will be to connect these infant gestures with adult human gestures, and/or with signs. Yet another question will be to assess the extent of iconicity in ape gestures, as proposed in connection with the pointing and pantomime of bonobos by several groups of researchers (e.g. Genty and Zuberbühler 2014, Douglas and Moscovice 2015).

□ *Summary*

In sum, we have seen that a formal linguistic approach can be fruitfully applied to animal communication systems, where recent research has covered quite a lot of ground: from a syntax perspective, birdsongs provided rich empirical data, whereas a linguistically inspired study of primate signals has contributed to the understanding of call and gesture meanings in a range of monkey species, and raised questions concerning the evolution of animal meanings.

Several points are worth highlighting with regards to the linguistically inspired analysis of animal communication. First, the formal linguistic approach has proven useful to regiment theoretical analyses and force them to be precise about their predictions; at the same time, it has allowed researchers to uncover new generalizations and problems – pertaining for instance to the formal classification of bird syntax, or to the potential existence of implicatures in monkey calls. Second, the issue of the division of labor among different modules (e.g. syntax, semantics, pragmatics) has been shown to clearly arise in the study of animal communication systems; interface issues can be particularly important, as when one must decide whether a certain meaning component is due to lexical semantics or to pragmatic enrichment (as in Campbell's monkeys). Third, while not addressed in this article, multimodality can arise in some animal systems, such as ape communication, which involves both gestures and calls (see Genty et al. 2014, among others). Fourth, the demonstrated fruitfulness of the general methods and questions resulting from a broadly inspired linguistic approach should not lead to the conclusion that animal communication shares important non-trivial properties with human language. In most cases, the conclusion is just the opposite: bird syntax is nothing like human syntax, and despite the possible existence of implicatures in monkeys, the semantics of their calls has little in common with human language utterances. Fifth, issues of biological evolution, which are notoriously difficult to address for human language, are increasingly giving rise to precise findings in the study of animal communication systems.

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