Context and Meaning in Titi Call Sequences*

Philippe Schlenker[1], Emmanuel Chemla[2], Cristiane Cäsar[3], Robin Ryder[4], Klaus Zuberbühler[5]

March 1, 2015

Abstract. Cäsar et al. 2013 show that the structure of Titi monkey call sequences can, with just two call types (A and B), reflect information about predator type and predator location. Using the general methods of Schlenker et al. 2014, we ask what these facts show about the 'linguistic' structure of Titi calls. We first demonstrate that the simplest behavioral assumptions make it challenging to provide *lexical specifications* for A- and B-calls: B-calls rather clearly have the distribution of general alarm calls; but A-calls are also found in highly heterogeneous contexts (e.g. they are triggered by 'cat in the canopy' and 'raptor on the ground' situations). We discuss two possible solutions to the problem. One posits that entire sequences are endowed with meanings that are not compositionally derived from their individual parts (a related idea was proposed by Arnold and Zuberbühler to analyze *pyow-hack* sequences in Putty-nosed monkeys). The second analysis combines a very simple compositional analysis with some more sophisticated assumptions about the environmental context in which the calls are used; specifically, we argue that the B-call is a general alarm call, that the A-call is used for serious non-ground threats, and that they are combined by the simplest (conjunctive) rule; but their interaction with the context conspires to make it possible for call sequences to reflect information about predator nature and predator location.

1 Introduction

Cäsar et al. 2013 show that the structure of Titi monkey call sequences can, with just two quiet call types (A and B), reflect information about predator type and predator location. Using the general methods of Schlenker et al. 2014, as well as Cäsar et al.'s raw data, we ask what these facts show about the 'linguistic' structure of Titi calls. We first demonstrate that the simplest behavioral assumptions make it challenging to provide *lexical specifications* for A- and B-calls: B-calls rather clearly have the distribution of general alarm calls; but A-calls are also found in highly heterogeneous contexts (e.g. they are triggered by 'cat in the canopy' and 'raptor on the ground' situations). We discuss two possible solutions to the problem. The first analysis posits that entire sequences are endowed with meanings that are not compositionally derived from their individual parts (a related idea was proposed by Arnold and Zuberbühler (2006, 2008, 2012, 2013) to analyze *pyow-hack* sequences in Putty-nosed monkeys). The second analysis combines a very simple compositional analysis with some more sophisticated assumptions about the environmental context in which the calls are used; specifically, we argue that the B-call is a *general alarm* call, that the A-call is used for *serious non-ground threats*, and that they are combined by the simplest (conjunctive) rule; but their interaction with the context conspires to make it possible for call sequences to reflect information about predator nature and predator location.

---

* [Acknowledgments to be added when the paper is final.]
[1] Institut Jean-Nicod (ENS - EHESS - CNRS), Département d'Etudes Cognitives, Ecole Normale Supérieure, Paris, France; PSL Research University ; New York University.
[2] Laboratoire de Sciences Cognitives et Psycholinguistique (ENS, EHESS, CNRS), Département d'Etudes Cognitives (Ecole Normale Supérieure – PSL Research University)
[3] School of Psychology and Neuroscience, University of St Andrews, St Mary's Quad, St Andrews, Fife, United Kingdom ; Bicho do Mato Instituto de Pesquisa, Belo Horizonte, Brazil.
[4] Centre de Recherche en Mathématiques de la Décision, Université Paris-Dauphine, Paris, France.
[5] Centre for Cognitive Science, University of Neuchâtel, Neuchâtel, Switzerland ; School of Psychology & Neuroscience, University of St Andrews, St Mary's Quad, St Andrews, Fife, United Kingdom.

2 Titi Sequences

In Cäsar et al.'s field experiments, the two factors *predator = {cat; raptor}* and *location = {on the ground; in the canopy}* gave rise to four types of sequences obtained with just two quiet calls, the A-call and the B-call, as represented in slightly simplified form in (1) (note that Titis have other quiet and loud calls, as described in Cäsar 2011). In each case, our generalizations are based on the first 30 calls of the sequences triggered by the various situations. The restriction to 30 calls is motivated by the fact that, after that point, the patterns obtained with A and B calls just repeat the end of the 30-call sequence (although in response to terrestrial predators, Titis might after a while produce some different, louder calls). When average lengths are given, they are thus computed on the basis of these truncated sequences as well, hence with a maximum length of 30 for any given sequence.

(*Notation:* if X is any call, X^+ represents a series of at least one X-call, and X^{++} a series of at least two X-calls. We write $\underline{X^+}$ and $\underline{X^{++}}$ for series that display these patterns with up to 3 extraneous calls interspersed.)

(1) **Model predator experiments**

a. Raptor in the canopy:	A^{++} (4/5 sequences; the 5th contains interspersed O-calls; average length of the 5 sequences=26.8 calls)
b. Raptor on the ground:	$\underline{A^{++}B^{++}}$ (5/7 sequences; 2/7 have the form A^+)
c. Cat in the canopy:	$\underline{A\ B^{++}}$ (4/6 sequences; 1/6 has the form X A B^{++} with an unidentified call X)
d. Cat on the ground:	B^{++} (5/5 sequences)

In addition, Cäsar collected naturalistic data, which provide further useful information and is summarized in simplified form in (2).

(2) **Naturalistic observations**

a. Flying raptor:	A^+	(19/20 sequences; average length of the 20 sequences = 2.2 calls)
b. Calling or perched raptor:	$\underline{A^{++}}$	(9/9; average length of the 9 sequences = 15.8 calls]
c. Capuchin in tree:	Diverse:	A^{++}, A^{++} B^{++} A^{++}, etc with C-calls interspersed (see Appendix)
d. Non-animal-related (foraging/descending/feeding):	B^{++}	(13/16)

Simple inspection shows that the stereotyped call sequences in (1) encode information about both predator threat and predator location. Should we conclude that Titi monkeys can associate a complex syntax to complex meanings? We will argue that this is unlikely, and that the generalizations in (1) and (2) are compatible with an analysis in which each call has a simple meaning that pertains to the precise moment at which it is uttered; on this view, the complexity of the call sequences is due at least as much to the complexity of the environmental context – and the fact that it changes as calls are uttered – as to the Titi linguistic system *per se*.

3 Monkey Meanings: semantics, pragmatics and world knowledge

Schlenker et al. 2014 attempt to apply the general methods of formal linguistics to two apparent 'dialects' of male Campbell's monkey alarm calls. While they do not claim that there is any (non-trivial) formal resemblance between Campbell's and human semantics, they do explore formal models in which each call (i) has a lexically-specified meaning; which (ii) can be enriched by rules of competition among calls; and (iii) modulated by world knowledge. In effect, they make use of three basic modules of meaning that are standardly posited in analyses of human languages: literal meaning (= semantics); scalar implicatures, derived by assuming that under certain conditions the most informative sentence compatible with a situation is used (= a part of pragmatics); and world knowledge, which allows speakers to draw inferences that go beyond the information contributed by semantics and pragmatics alone.

Let us give a simple example to illustrate each module. It is uncontroversial that a speaker's mental dictionary must provide for a meaning difference between *or* and *and*; these are usually given the truth conditions in (3)

(3) **Literal Meaning**
a. *S* ***and*** *S*' is true if and only if *S* is true and *S*' is true
b. *S* ***or*** *S*' is true if and only if *S* is true, or *S*' is true, or both ('inclusive *or*')

Clearly, sentences of the form *S and S*' and *S or S*' give rise to all sorts of inferences which do not just depend on the meaning of *S*, *S*' and *and/or*, but also on what speakers know about the world. Two simple examples are given in (4).

(4) **World Knowledge**
a. John has been to Paris and he has been to Rome
=> John hasn't been to Paris and Rome at the same time
b. John is in Paris or he is in Rome
=> John isn't both in Paris and in Rome

–While an utterance of (4)a gives rise to the inference that John has been to Paris and to Rome *but not at the same time*, there is certainly no need to add a negative temporal component to the lexical entry of *and* in (3)a in order to account for this observation: world knowledge guarantees that John couldn't have been in two places at the same time, and thus this inference need not be attributed to the semantics.
–The exclusive inference in (4)b can be treated in the same way. We might initially think that the *not both* inference argues for a different lexical entry for disjunction, one in which *or both* in (3)b is replaced with *but not both* ('exclusive *or*'). But a moment of thought suggests that here too world knowledge could just as well conspire with the lexical entry in (3)b to yield the observed inference, as John could not in Paris and Rome at the same time.

Other cases have been taken to argue for a third module, however, one which is distinct both from literal meaning and from world knowledge. A case in point is given in (5).

(5) **Pragmatic Strengthening [here: Scalar Implicatures]**
I'll invite John or Mary
=>? I'll invite John or Mary but not both

The exclusive inference in (5) initially looks like the one we had in (4)b, but upon further reflection it cannot be derived from world knowledge: in most situations, there is no reason whatsoever to think that the speaker couldn't both invite John and Mary. An alternative analysis would be to take this inference to argue for a revision of the lexical entry in (3)b, one in which exclusive *or* replaces inclusive *or*. But this option has been disfavored in recent linguistic theorizing, among others because it fails to account for the fact that it is by no means contradictory to say: *I'll invite John or Mary – in fact, I'll invite them both*. Without going into the details of a sophisticated line of argument, suffice it to say that contemporary theories are almost always based on the idea that the inference is due to competition between *or* and *and*: the sentence *I'll invite John or Mary* is compared to the alternative obtained by replacing *or* with *and*. The sentence *I'll invite John and Mary* is strictly more informative than the sentence *I'll invite John or Mary*. Hence one infers that the reason the speaker didn't choose the more informative version was that it was likely false. The result of this procedure is outlined in (6) (see Horn 1972 for some seminal ideas, and Schlenker 2014 for a recent survey).

(6) a. A sentence *S* containing *or* is compared with alternatives *S*' obtained by replacing one or several occurrences of *or* with *and*.
b. If a sentence *S* is uttered and an alterantive *S*' to *S* is strictly more informative than *S*, one can usually infer that *S*' is false.

Briefly, Schlenker et al. 2014 make use of these three modules to analyze Campbell's alarm calls from the Tai forest, where the main predators are leopards and eagles:

Semantics: They provide simple lexical entries on which *krak* is a general alarm call, and *hok* is a non-ground alarm call, and *krakoo* is a weak alarm call.

Pragmatics: They posit a rule of competition between *krak, krakoo* and *hok*, whose effect is that an utterance of *krak* usually (but not invariably) gives rise to the inference that *hok* and *krakoo* could not have been used. In the end, this yields the inference that *there was a serious ground alarm*: 'serious' because otherwise *krakoo* would have been used; and 'ground' because otherwise *hok* would have been used.

World knowledge: Finally, they posit that the main serious ground alarm in the Tai forest is due to leopards, hence the impression that *krak* is a leopard alarm call.

They argue that their analysis has the advantage of explaining why *krak* does have a few aerial uses in the Tai forest; and more importantly, why on Tiwai island, where eagles but not leopards are present, *krak* is used as a general call, with its semantic meaning and without pragmatic strengthening.[3]

World change: Importantly, the preferred analysis developed in Schlenker et al. had to rely not just on word knowledge but also on world *change* to provide an analysis of complex sequences. In brief, they had to explain why one and the same sequence could contain one or several *hoks*, as well as *krak-oo's*. Given the 'weak alert' meaning of the latter, these sequences should come out as near-contradictions. The authors' solution was to relativize the meaning of each call to the precise time at which it was uttered, thus circumventing the problem of contradictions – with the result that the subjective seriousness of an alarm could change within the course of the utterance of a single sentence. While this was a rather theory-internal measure in Campbell's semantics, it will prove crucial in our analysis of Titi sequences.

4 The Titi Challenge: Lexical Specifications

The Titi generalizations in (1) and (2) pose a challenge for a semantic analysis based on simple (we'll soon say: simplistic) assumptions about the environment. In a nutshell, the problem is that the B-call occurs in contexts that are so diverse that it seems to be a general alarm call, with a very weak lexical specification. But it turns out that within predator contexts the A-call *also* occurs in environments that fail to form a natural class, and hence it seems to function as a general predator alarm call. But if this is so, within predator contexts the difference between A-calls and B-calls becomes hard to analyze.

It is immediate that the lexical contribution of B-calls must be extremely weak, since they appear both in non-predation ((2)d) and in predation ((1)b, c, d; (2)d) contexts; furthermore, within predation contexts they occur both in eagle ((1)b) and in leopard ((1)c, d) contexts, and in contexts in which the threat is on the ground ((1)b) as well as in the canopy (((1)c). This suggests the lexical entry in (7).

(7) **B-call**
B is applicable if and only if there is an alert.

Difficulties arise when we notice that the A-call also occurs in heterogeneous environments. While in our data A-calls are not used in non-predatory situations, within predator-related situations they occur both in 'raptor on the ground' situations ((1)a) and in 'cat in the canopy' situations ((1)c). It is hard to see what these two situations could have in common besides being situations of predation. So it would seem reasonable to posit the lexical entry in (8):

(8) **A-call (1st try)**
A is applicable if and only if there is a predator-related alert.

Although A- and B-calls have different lexical specifications according to the rules in (7) and (8), *within predator contexts* it is entirely unclear what could distinguish them from each other. We could try to add to our analysis a pragmatic component as in (9), with the prediction in (10).

(9) **Competition among calls**
a. A- and B- calls compete with each other.
b. Since A is more informative than B, if a B-call is produced, infer that the A-call was not applicable at the same moment and in the same situation.

[3] World knowledge plays a crucial role to determine whether pragmatic strengthening should be applied or not. In a nutshell, Schlenker et al. posit that the reason pragmatic strengthening fails to be applied on Tiwai island is that it would yield a strengthened meaning which is almost never applicable, because there are no ground predators in that environment.

(10) **Prediction of (9) given (7) and (8)**
When pragmatic strengthening is applied, the B-call should *only* be applicable when there is a non-predator related alert (since in predator-related alerts the A-call is more informative).

Given the lexical entries in (7) and (8), this pragmatic component has an undesirable consequence: the B-call is predicted not to normally arise in situations of predation, as stated in (10). The heart of the matter is that while the A-call is more informative than the B-call, its lexical specification is still very weak. And since the competition rule in (9) has the effect of enriching the meaning of B with the *negation* of A, the result is an enriched meaning for B which is just too strong, as it is predicted to not be applicable in situations of predation.

It was noted by Cäsar et al. 2013 that the first position in a sequence is somehow special, as it is often followed by a long pause, especially in non-stereotypical situations (raptor on the ground; cat in the canopy - see Cäsar et al. 2013, supplementary materials, figure 3S). Could we improve our analysis if we allowed calls to have different meanings in the first position and in the rest of sequences? As it turns out, this wouldn't help. For with respect to the first position, the B-call occurs both in situations of predation ((1)d) and in situations of non-predation ((2)d), which suggests that *even relative to the first position* it functions as a general alarm call. And the problem we had with the A-call does not change a bit when we restrict attention to the first position, since we get an initial A-call both in 'raptor in the canopy' and 'cat on the ground' situations, which again suggests that it has a general predator-related function.

5 Two Theories

We believe there are two natural directions to explore to solve the problem we just laid out. One is to posit that the meaning of an entire sequence is not compositionally derived from the meaning of the individual calls it contains, but rather is obtained 'holistically'. An alternative is to posit that the meaning of a sequence *is* compositionally derived, but to rely more heavily on assumptions about the environments, by (i) making greater use of world knowledge in connecting literal meanings to their conditions of use, and by (ii) relativizing the meaning of a call to the precise moment at which it is uttered.

To be more specific: we will posit that (i) the A-call is a (serious) non-ground alarm, and that the reason it occurs in 'raptor on the ground' situations is that even in these cases the *threat* (as opposed to the *predator*) is non-ground-related; and that (ii) the nature and the level of the threat can change as a sequence is produced – which will for instance connect the number of A-calls to the duration of the threat.

5.1 A non-compositional theory

In a series of influential papers, Arnold and Zuberbühler (2006, 2008, 2012, 2013) argued that Putty-nosed monkeys have *pyow* calls that serve as general alarms or attention getters, *hack* calls that are usually related to the presence of aerial threats, and *pyow-hack* sequences that are predictive of group movement. Arnold and Zuberbühler argue that *pyow-hack* sequences are syntactically combinatorial because they are made from individual calls; but that they are not compositional, because their meaning does not seem to be derivable from that of their individual parts. Importantly, *pyow-hack* sequences are made of a small number of *pyows* followed by a small number of *hacks*, but the number of calls of each sort appears to be flexible – and to have the same effect on group movement when the total number of calls is kept constant. Thus they showed in field experiments that the distance travelled was roughly the same when the female Putty-nosed monkeys heard a series of 3 *pyows* followed by 3 *hacks*, 1 *pyow* followed by 5 *hacks*, or 5 *pyows* followed by 1 *hack*. While one could posit highly disjunctive rules to cover all these cases, it seems more economical to posit that the semantics is not sensitive to the precise number of repetitions, and to give lexical entries such as those in (11), where as before X^+ stands for an arbitrary number of consecutive occurrences of call X. (Note that Arnold and Zuberbühler only argue that *pyow-hack* sequences should be given a non-compositional treatment, but once this device is available, one may extend it to pure *pyow* and pure *hack* series as well – which is why in (11)a, b we leave it open whether individual calls or entire call sequences should be given a meaning.)

(11) **Putty-nosed calls: syntactic combination without semantic combination?**
a. P / P^+ series are used as general alarms.
b. H / H^+ series are usually associated with the presence of aerial threats.
c. P^+H^+ sequences are usually predictive of group movement.

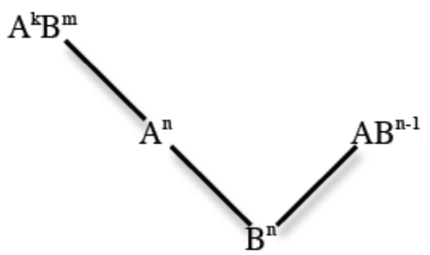
Given this precedent, we could try to extend the method of whole sequence meanings to Titi calls. As an initial attempt, we could take the context descriptions in (1) and (2) to come close to the meanings of entire sequences. On a technical level, we specify meanings for *maximal* sequences, for otherwise we would run into ambiguities, as it wouldn't be clear whether a sequence $A^{++}B^{++}$ should be analyzed as an A^{++} sequence followed by a B^{++} sequence, or as a primitive $A^{++}B^{++}$ sequence; by specifying meanings for *maximal* sequences, the first option is precluded. To further refine the analysis, we may make use of rules of competition among entire call sequences in order to have a leaner analysis, for instance the one illustrated in (12)-(13).

(12) **Non-compositional Titi meanings**
a. A maximal sequence of the form B^{++} is applicable if and only if there is an alert.
b. A maximal sequence of the form A^{++} is applicable if and only if there is a non-ground predator.
c. A maximal sequence of the form $A^{++}B^{++}$ is applicable if and only if there is a non-ground predator on the ground.
d. A maximal sequence of the form AB^{++} is applicable if and only if there is a ground predator in a non-ground position.

(13) **Whole sequence competition**
a. A Titi sequence competes with all sequences obtained by replacing (call for call) any number of A's with B's and any number of B's with A's.
b. If a sequences *S* is uttered and competes with a more informative sequence *S*', one can infer that *S*' wasn't applicable.

The (modest) benefit of this analysis is that it makes it possible to assign very simple meanings to the B^{++} and A^{++} series, with the pattern of precedence illustrated in (14). The point is that the competition principle in (13) will lead to an *enrichment* of these simple meanings by way of inferences that A^n and A^kB^m could not have been used; the results are illustrated in (15).

(14) **Informativity relations among Titi sentences**
according to (12) (higher = strictly more informative) for any n ≥ 3 and for any k, m ≥ 2 such that k+m = n



(15) **Strengthened Titi meanings**
For any n ≥ 3 and for any k ≥ 1 and m ≥ 2,[4]
a. for any sentence *S* of the form S = B^n, S can be used
if and only if there is an alert but no non-ground predator (or else A^n would have been used) and no ground predator in a non-ground position (or else AB^{n-1} would have been used),
if and only if there is a ground predator in a ground position;
b. for any sentence *S* of the form S = A^n, S can be used
if and only if there is a non-ground predator but not a non-ground predator on the ground (or else A^kB^m would have been used),
if and only if there is a non-ground predator in the canopy;

[4] The conditions on k and n are more stringent in (14) than in (15) because in (14) we wish to guarantee that A^kB^m has the right number of calls to serve as a competitor to A^n and to B^n; since competitors are defined in (13) by call-for-call replacement replacement, this leads to the condition the condition k+m = n.

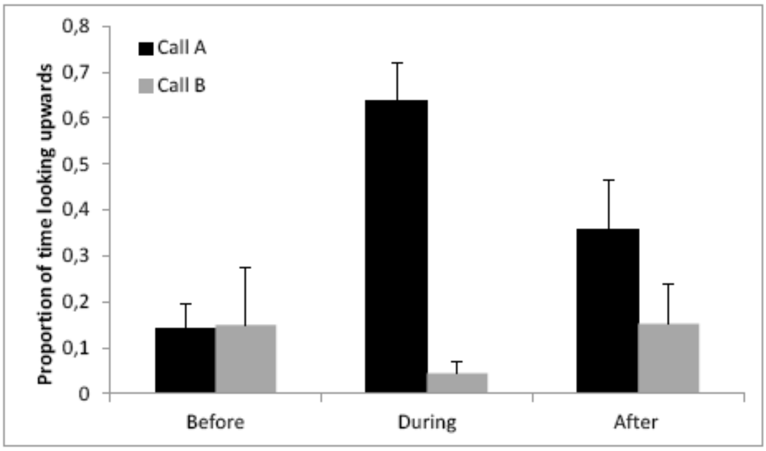
c. for any sentence *S* of the form S = $A^k B^m$, S can be used iff there is a non-ground predator on the ground;
d. for any sentence *S* of the form S = AB^n, S can be used iff there is a ground predator in a non-ground position.

Still, we believe that this theory has three main flaws.

–*Explanatory power:* The analysis as it stands re-states in slightly improved form (due to mechanisms of competition) the generalizations we saw in (1). A symptom of this problem is that it has nothing to say about sequences whose form is slightly different from that of the sequences listed in (12). Thus this analysis lacks explanatory force.

–*Initial reactions:* Cäsar 2012a notes that after hearing an A-call, the Titi monkeys very quickly start looking upwards, as shown in (16) and (17) (latency is computed relative to the start of the playback). Presumably this fast reaction is also triggered $A^{++}B^{++}$ sequences, which according to (12)c provide information about non-ground predators that on the ground. But this suggests that what is crucial about A-calls is not so much their raptor-related content as the information they provide about a non-ground threat.

(16) 'Looking upwards' as a reaction to A- vs. B-calls (from Cäsar et al. 2012a figure 3)



(17) Latency of A- vs. B-calls (from Cäsar et al. 2012a figure 2; latency is computed after the start of the playback)

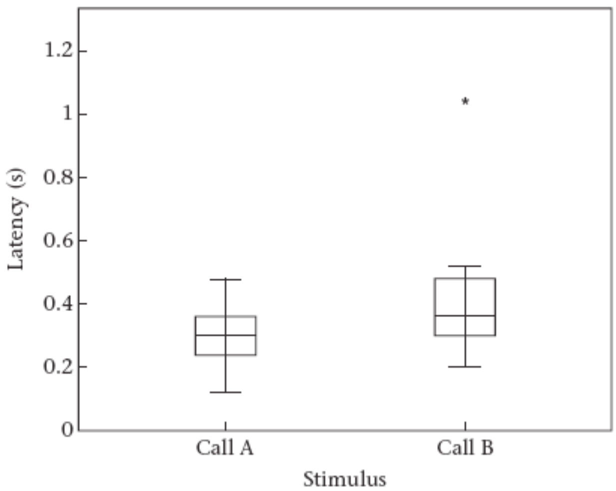


Figure 2. Box plots indicating the latencies in response to the different playback types. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range, and the asterisk indicates an extreme case. Number of trials: 10 for call A and 12 for call B.

–Timing: Titi sequences are not very fast, with an average inter-call interval of 1.4s. (12)b-c above posits distinct meanings for A^{++} vs. $A^{++}B^{++}$ sequences in order to explain why A^{++} is found in 'raptor in the canopy' situations while $A^{++}B^{++}$ is found in 'raptor on the ground' situations. It is thus clear that one must wait at least until one has heard a B-call to tell that one is hearing an $A^{++}B^{++}$ rather than an A^{++} sequence. But in 'raptor on the ground' situation, when B-calls are produced, the first B-call appears on average after the 12th position in the sequence (average position: 12.6); very roughly, this gives an average waiting time of 16-17s or so before one hears the first B-call after the first call is produced.[5] This would seem like a very long time to wait to determine which elementary meaning one is exposed to – hence a dilemma. If the receivers of the message cannot start reacting before they have determined which of the two sequence types they are hearing, how can such a meaning assignment be adaptive?[6] Alternatively, it could be that the informational contents of $A^{++}B^{++}$ and A^{++} sequences license the same initial reaction – so that the receiver need not decide which sentence it is hearing before starting to react. But if so, shouldn't we take that initial reaction to provide a key to the semantic content of the initial part of the sequence within a (more) compositional theory? This is what we will propose in our compositional theory, with the claim that A-calls call attention to a serious non-ground threat.

We conclude that the non-compositional analysis of Titi sequences has significant flaws, and that an alternative theory should be explored.

5.2 A compositional alternative

We will now circumvent the problems we encountered with our initial specifications of compositional meanings by assuming (i) that the A-call does not provide information about the nature of the predator and its location, but rather about the *appropriate reactions* to the relevant threat, and (ii) that the composition of sequences in part reflects the way in which the environment changes as a sentence is uttered. Specifically, we will assume that the A-call is specified for *serious non-ground alerts*, and that the reason we find an initial A^{++} sequence in 'raptor on the ground' situation is that raptors attack by flying, and thus that *even* when a raptor is on the ground the threat isn't a ground one. As for the fact that B^{++} sequences can follow A^{++} sequences, this will be taken to reflect the fact that in some cases the threat level is taken to diminish after the appearance of an initial trigger, and thus that the 'serious non-ground alert' content of the A-call stops being applicable after a while, leaving B as the only contender.

To develop the analysis in more detail, we will need three assumptions that have some independent motivation.

(18) a. A raptor hunts by being perched or by flying; a raptor on the ground is not in a hunting position.
b. Cats become less dangerous once they have been detected (because they are ambush rather than pursuit hunters).
c. Capuchins are dangerous even if they have been detected (because they are pursuit hunters).

About (18)a: one can infer from descriptions of eagle hunting techniques to hunt monkeys that they attack from above, not from the ground (see Shultz and Thomsett 2007 for eagles in the Tai forest[7]).
About (18)b: an example from a different part of the world is given in Zuberbühler et al. 1999, who show "after detection and high alarm call rates" a radio-collared leopard "gave up its hiding location

[5] This is a rough approximation, obtained by multiplying 12.6-1 (= 11.6 = average the number of inter-call intervals heard between the first call of the sequence and the first B-call) by 1.437, the average inter-call length over *all* sequences; the result is 16.7s.
[6] Note that the lexical meaning of A^{++} is weaker than (and hence compatible with) that of $A^{++}B^{++}$. One could thus argue that the informational component these two sequence types have in common licenses the appropriate reaction as long as the ambiguity has not been resolved. But our analysis crucially hinges on the fact that the lexical meaning of A^{++} is pragmatically enriched with the negation of $A^{++}B^{++}$. For behavioral purposes, it is this enriched meaning that presumably matter. But the enriched meaning of A^{++} meaning is clearly incompatible with that $A^{++}B^{++}$, which means that the proposed strategy won't help much.
[7] The authors describe both a 'searching' and a 'sit-and-wait' strategy, but it seems clear that even the latter involves attacks from above (as the authors write, the predators 'drop down' on the monkeys).

and left the group significantly faster than would be expected by chance", which would suggest that detection was sufficient to considerably lower its chances of success (see also Zuberbühler and Jenny 2007).
About (18)c: Fedigan 1990 describes hunting strategies by Capuchin monkeys which rely on *chasing* a prey.

Our semantics will be extremely simple: each call will contribute a simple meaning to a sequence; when several calls are present, they will be composed conjunctively, which is the simplest mode of composition (= each call contributes its meaning independently from the other calls). Importantly, however, we take into account the fact that call rates are relatively slow, and thus that different calls provide information about the environment *at different times*. For this reason, the applicability conditions of calls are relativized to utterance times. It should be noted that a side effect of this relativization to times is that repetition of calls is not semantically vacuous: each repetition of an alarm call makes a new claim, namely that the relevant alarm holds *at the time of utterance of that call*.

On this view, successive calls are separate sentences making claims about different moments, as stated in (19). (19)a is just the statement that B is a general alarm call. (19)b encodes the treatment of A as a serious non-ground alert. If we wish to compute the cumulative semantic effect of a call sequence, we can use the rule in (20), which specifies that the various calls *evaluated at their precise time of utterance* are combined conjunctively.

(19) Semantics of Titi calls (partial: A- and B-calls only)
For any time t,
a. B uttered at t is true if and only if there is an alert at t.
b. A uttered at t is true if and only if there is a serious non-ground alert at t.

(20) Call 'composition'
If x is a call and S is sequence of calls,
x S uttered at t is true if and only if x uttered at t is true and S uttered at t+1 is true.

Two examples are given in (21).

(21) Two examples
a. B uttered at time 0 is true if and only if there is an alert at time 0.
b. AB uttered at time 0 is true if and only if
A uttered at time 0 is true and B uttered at time 1 is true, i.e. if and only if
there is a serious non-ground alert at time 0 and there is an alert at time 1.

(21)a is unexceptional; (21)b displays a simple case in which the two calls are evaluated at different times: time 0 for A, time 1 for B.

It is immediate that the distribution of B-calls must be further constrained – for without addition, the semantics would lead one to expect that the call can arise in all situations, contrary to fact. The natural solution is to adopt the rule of competition we discussed in (9).

(22) Pragmatics of Titi calls
a. A- and B-calls compete with each other following the rules in (9).
b. Derived result: if B is uttered at time t, one can infer that (i) there is an alert at time t, but not (ii) a serious non-ground alert (or else the A-call would have been used).

Importantly, we do not get the undesirable result we had in our initial discussion, where A was specified as a predator call and B was thus incorrectly strengthened into a non-predator call. The strengthening we now obtain is far more adequate: B should not be uttered at time t if there is a serious non-ground alert at that time.

Let us now see how our hypotheses can derive the patterns we observe. Let us start with the model predator experiments in (1)-(2), repeated in condensed form in (23).

(23) **Simplified Generalizations**

		a. Raptor	b. Cat	c. Capuchin	d. Non-predator related
Experimental	Canopy	(i) A^{++} (mean=26.8	(i) AB^{++}		

		calls)			
	Ground	(ii) $\underline{A^{++}B^{++}}$	(ii) B^{++}		
Naturalistic		(iii) *Flying:* A^{+} (mean=2.2 calls) (iv) *Calling or perched:* $\underline{A^{++}}$ (mean=15.8 calls)		*In tree:* A^{++}, $A^{++}B^{++}A^{++}$, etc, with C-calls interspersed (see Appendix)	*deer, foraging/descending* B^{++}

Raptor situations: The generalizations (23)a(i), (iii) and (iv) are unsurprising in view of our hypotheses about eagle hunting techniques in (18)a. First, a model raptor in the canopy or a perched raptor present serious non-ground threats, and the threats should be taken to persist in time since these are typical hunting positions – hence the fact that the series are long. Second, series of A-calls are shorter in the naturalistic 'flying raptor' situations in (23)a(ii) (Mean number of A's: 2.2) than in the naturalistic 'calling/perched raptor' (M=15.8 A's, t = 3.2899, df = 8.143, p = .01076) situations in (23)a(iv) or in the experimental 'raptor in canopy' situations in (23)a(i) (M=26.8, t = 11.6088, df = 4.281, p = .0002138); this is presumably because a raptor that flies away is a briefer threat than the immobile raptors in typical hunting position (it might also be that in experimental situations the model raptor remains perched longer than in naturalistic ones, although it might become clear at some point that it is not a normal living raptor).[8] Finally, the pattern in (23)b(ii) is expected if we remember that a raptor on the ground will attack (if it does) by flying, as stated in (18)a. Therefore the initial A^{++} we find is unsurprising and provides the most urgent message first, as a danger may be coming from above.

Since immobility on the ground is not a typical hunting position, it is also unsurprising that after a while the threat stops being considered as serious – presumably because a raptor would not normally remain motionless on the ground for long periods of time. As mentioned above, the first B-call in 'raptor on the ground' situations occurs on average in position 12.6 in the sequence – with a possible estimate of 16-17s after the first call. This might give enough time to the caller to decide that the threat isn't too serious any more; if so, it is because the A-call is specified for *serious* non-ground threats that it stops being applicable after that time, with the result that B-calls start being used instead. By the logic of pragmatic competition, this is the only case in which we see B-calls for raptor-related threats.

Cat situations: In 'cat on the ground' situations, only the B-call can be used, hence the B-series in (23)b(ii). The production of an A-call (specified for a 'serious non-ground alert') at the beginning of 'cat in the canopy' situations should give us pause. Given our assumptions, it can be explained:
–When a cat is detected in the canopy, it represents a serious non-ground threat, hence the production of an A-call.
–As a consequence of this A-call, the cat can be taken to be detected. As a result, the threat level diminishes, in accordance with (18)b. Because the A-call is specified for *serious* non-ground threats, it can't be used any more, with the result that only the B-call can be used.

Capuchin situations: Naturalistic capuchin situations give rise to a diversity of calling sequences, some of them with quite a few A-calls. This is strikingly different from the stereotyped AB^{++} sequences we found in 'cat in the canopy' model experiments. It is thus notable that two mammal predators in non-ground situations give rise to such different calling behaviors. Now one source of the difference might be that real capuchins move in ways that model leopards don't.[9] But an additional explanation might lie in the difference between leopard and capuchin hunting strategies outlined in

[8] Note that there are significantly fewer calls in (naturalistic) 'calling/perched raptor' than in (experimental) 'raptor in the canopy' situations: (t = 2.3926, df = 11.166, p = .03539). It could be that that in the former case the trigger disappears more quickly than in the second, which involves raptor models.

[9] Note however that some naturalistic situations give rise to stereotyped sequences, as can be seen in the naturalistic Eagle-related sequences in (23)a(iii)-(iv).

(18)b,c: capuchins *continue* to be dangerous even after they have been detected, hence we have no reason to expect the AB^{++} pattern we found in 'cat in the canopy' situations. While this doesn't explain the *details* of the complex patterns we find in capuchin situations, it does give us a way to address an initially surprising difference.

Non-predatory situations: It is clear that in situations that do not involve serious threats the A-call cannot be used, hence the fact that we only find B-calls in these cases.

(We leave for future research an analysis of the C-call, which might conceivably be a 'group movement' call – but it is too early to make precise pronouncements.)

6 Conclusion

While the present study adds to the general program of applying explicit formal methods to the syntax and semantics of call sequences, it brings attention to the importance of assumptions about the environment. With our initial hypothesis that calls directly convey information about predator type and/or predator location, we were not able to provide a coherent meaning for A- and B-calls, and we had to resort to a somewhat unappealing theory in which entire call sequences had a non-compositional meaning. Arguably, a better and simpler theory can be obtained if we make use of more sophisticated assumptions about the environmental context. Two proved particularly crucial: first, we assumed that a raptor on the ground still signals the presence of a non-ground threat; second, we assumed that the meaning of calls is relativized to the precise time at which they are uttered, with the result that the composition of a sequence sometimes reflects the way in which the environmental context changes as the sequence is uttered. It should be added that besides semantics and the environment, pragmatic competition among calls played an important role in our explorations, since this mechanism was crucial to explain why B-calls are not found in all situations. Thus the general issue of the division of labor between semantics, pragmatics and environment/world knowledge turned out to be the main issue in this study – as it was (in a different way) in Schlenker et al.'s (2014) study of male Campbell's monkey calls.

Appendix. Sample Sequences

We provide below sample sequences obtained in various situations (up to the 30th call in each case). For the data obtained in field experiments with raptor and cat models, as well as for naturalistic raptor situations, and for situations of feeding/foraging/descending, we provide the first half of each block[10]. For naturalistic Capuchin situations and for non-predatory situations, we provide all our transcribed data. (We do not provide data from field experiments with tayra, puma and boa models, as these are the object of a separate study.)

Color code: A calls = orange; B calls = green; C calls = yellow

- *Location experiments with Raptor vs. Cat Models (first half of each block)*

–Raptor in the canopy

Raptor canopy	Stimulus	9/26/08	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A
Raptor canopy	Stimulus	9/19/08	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A											
Raptor canopy	Stimulus	9/14/09	M	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A

–Raptor on the ground

Raptor ground	Stimulus	6/9/10	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	C	C	C	B	B
Raptor ground	Stimulus	6/24/10	D	A																													
Raptor ground	Stimulus	6/17/11	LD	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B
Raptor ground	Stimulus	6/31/10	M*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A

–Cat on the ground

Cat ground	Stimulus	8/14/09	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Cat ground	Stimulus	8/6/08	D	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Cat ground	Stimulus	9/22/09	M	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

–Cat in the canopy

Cat canopy	Stimulus	6/28/10	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Cat canopy	Stimulus	6/28/10	D	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Cat canopy	Stimulus	7/14/10	M	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

- *Raw Data: Naturalistic Raptor Situations (first half of each block)*

–Flying raptor

Flying Raptor	Real	6/10/10	A	A	A	A	A	A																									
Flying Raptor	Real	6/20/10	A	A																													
Flying Raptor	Real	6/20/10	A	A	A	A	A	A																									
Flying Raptor	Real	7/24/09	D	A	A	C																											
Flying Raptor	Real	8/5/08	D	A																													
Flying Raptor	Real	8/6/08	D	A																													
Flying Raptor	Real	6/2/09	D	A																													
Flying Raptor	Real	6/2/09	D	A																													
Flying Raptor	Real	6/2/09	D	A	A																												
Flying Raptor	Real	7/2/08	D	A																													

–Perched raptor

Perched Raptor	Real	10/10/08	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	
Perched Raptor	Real	5/25/10	M	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A

–Calling raptor

---

[10] Within blocks, sequences were ordered by alphabetical order (depending on the Titi group's name).

Calling Raptor	Real	6/29/10	A	A	A	A	A	A																									
Calling Raptor	Real	7/8/10	M	?	?	A	A																										
Calling Raptor	Real	7/10/09	M	A	A	A	A	C	C	A	A	A	A																				

- *Raw data: other animals (complete for Capuchins; samples for other animals)*

–Puma

Puma	Stimulus	11/5/09	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Puma	Stimulus	6/2/09	D	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Puma	Stimulus	13/16/09	M	B	B	B	B	NOT possible to code - CICADAS																									

–Capuchin in tree

Capuchin in tr	Real	6/26/10	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Capuchin in tr	Real	13/17/09	M	A	A	A	C	C	C	gr	C	gr	?	8Bs	A	?	?	?	1B?	A	A	C	?										
Capuchin in tr	Real	13/19/09	P	?	?	?	C	C	B	C	B	B	A	B	B	B	B	B	B	B	C	?	B	B	B	A	?	?	A	A	B	B	C
Capuchin in tr	Real	13/21/09	P	A	A	B	B	C	C	B	?	C	C	C	B	C	B	C	B	C	C	A	A	A	A	A	B	B					
Capuchin in tr	Real	6/27/09	R	?	C	C	C																										
Capuchin in tr	Real	6/27/10	R	A	A	A	A	A	A	A	B	B	B	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A

–Spotted cat on the ground

Spotted cat on	Real	9/1/08	M	B	B	B	B	B	B	B	B	B	B	C	B	C	C	B	B	B	B	B	B	B	B	B	B	B	B	C	B	B	B

–Deer on the ground

Deer on the	Real	13/15/09	M	B	B	B	C	B	B	B	B	B	B	B	B	B	C	C	C	C	C	C	C	C	C	C	B	C	C	C	B	B	C
			A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
			A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
			A	B	B	B	B	B	B	B	B+	B	B	B	B+	B+	B+	B+	B	B	B+	B+	B+	B	B	B	B	B	B	B	B	B	B
			D	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
			D	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

- *Raw Data: feeding, descending, foraging situations (first half)*

Feeding	Natural	6/24/09	GA	?	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B													
Descending/Foraging	Natural	6/24/09	GA	ANA	B	B	B	B	B	B	B	B	B	B	B	B																		
Descending	Natural	7/17/09	GA	AS	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B														
Descending	Natural	7/16/09	GA	ANA	B	B	B	B	B	B	B	B																						
Descending	Natural	7/1/08	GA	ANA	B	B	B	B	B	B	B	B	B	B	BS	BS	B	B	BS	B	B	BS	B	B	B									
Descending/Foraging	Natural	6/25/09	G1	DG	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B															
Descending/Feeding	Natural	7/2/08	G1	DI	B	B	B	B	B	B	B	B	B	B	B	B	Paw	Paw	Paw	Paw	Paw	B	B	B	B	B	B	B	B	B	B	B	B	B
Descending/Feeding	Natural	6/25/09	G1	DF/DI	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	x	B	x	B	B
Descending/Feeding	Natural	6/17/09	G1	DI	B	B	B	B	B	B	B	B	B	B	B	B	B	C	C	B	B	B	C	B	B	B	B	B	B	B	B	B	B	B
Descending	Natural	6/25/09	G1	DF	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B				
Descending/Feeding	Natural	5/14/10	G1	DG or D	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Feeding	Natural	7/3/08	G1	DF	B	B	B	B	B	B	B	B	B																					
Foraging	Natural	6/25/09	G1	DF	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

References

Arnold Kate, Pohlner Yvonne and Zuberbühler Klaus, 2001. Not Words but Meanings? Alarm Calling Behaviour in a Forest Guenon. *Developments in Primatology: Progress and Prospects* **35**: 437-468.

Arnold Kate, Pohlner Yvonne and Zuberbühler Klaus, 2008. A forest monkeys alarm calls to predator models. Behavioral. *Ecology and Sociobiology* **62**: 549–559.

Arnold Kate and Zuberbühler Klaus, 2006a. The alarm calling system of adult male putty-nosed monkey *Cercopithecus nictitans martini*. *Anim. Behav.* **72**: 643–653.

Arnold Kate and Zuberbühler Klaus, 2006b. Semantic combinations in primate calls. *Nature* **441**: 303.

Arnold Kate and Zuberbühler Klaus, 2008. Meaningful call combinations in a non-human primate. *Curr. Biol.* **18**(5): R202–R203.

Arnold Kate and Zuberbühler Klaus, 2012. Call combinations in monkeys: Compositional or idiomatic expressions? *Brain and Language* **120**(3): 303-309.

Arnold Kate and Zuberbühler Klaus, 2013. Female Putty-Nosed Monkeys Use Experimentally Altered Contextual Information to Disambiguate the Cause of Male Alarm Calls. *PLoS ONE* **8**(6): e65660. doi:10.1371/journal.pone.0065660.

Cäsar Cristiane, 2011. Anti-predator behaviour of black-fronted titi monkeys (Callicebus nigrifrons). Ph.D thesis, University of St Andrews.

Cäsar Cristiane, Byrne Richard, Hoppitt William, Young Robert J. and Zuberbühler Klaus, 2012a. Evidence for semantic communication in Titi monkey alarm calls. *Anim. Behav.* **84**: 405–411. doi:10.1016/j.anbehav.2012.05.010.

Cäsar Cristiane, Byrne Richard, Young Robert J. and Zuberbühler Klaus, 2012b. The alarm call system of wild black-fronted titi monkeys, *Callicebus nigrifrons*. *Behav. Ecol. Sociobiol.* **66**(5): 653–667. doi:10.1007/s00265-011-1313-0.

Cäsar Cristiane, Zuberbühler Klaus, Young Richard J. and Byrne Robert, 2013. Titi monkey call sequences vary with predator location and type. *Biol Lett* **9**: 20130535. doi:10.1098/rsbl.2013.0535.

Fedigan Linda M., 1990. Vertebrate Predation in Cebus capucinus: Meat Eating in a Neotropical Monkay. *Folia Primatol.* **54**(3-4): 196-205. doi: 10.1159/000156444.

Horn Laurence R., 1972. On the semantic properties of the logical operators in English. Ph.D.dissertation, University of California at Los Angeles, Los Angeles, California.

Schlenker Philippe: to appear, The Semantics/Pragmatics Interface. To appear in the *Cambridge Handbook of Formal Semantics*, eds. Aloni and Dekker.

Schlenker Philippe, Chemla Emmanuel, Arnold Kate, Lemasson Alban, Ouattara Karim, Keenan Sumir, Stephan Claudia, Ryder Robin and Zuberbühler Klaus: 2014, Monkey Semantics: Two 'Dialects' of Campbell's Monkey Alarm Calls. *Linguistics & Philosophy* 37, 6: 439-501. *DOI 10.1007/s10988-014-9155-7.*

Shultz Susanne and Thomsett Simon, 2007. Interactions between African crowned eagles and their primate prey community. In: *Monkeys of the Taï forest: an African monkey community*. (eds McGraw WS, Zuberbühler K, Noë R) Cambridge Univ. Press, Cambridge, pp 171–193.

Zuberbühler Klaus, Jenny David and Bshary Redouan, 1999. The Predator Deterrence Function of Primate Alarm Calls. *Ethology* **105** (6): 477–490. doi: 10.1046/j.1439-0310.1999.00396.x.

Zuberbühler Klaus and Jenny David, 2007. Interactions between leopards and monkeys. In: *Monkeys of the Taï Forest: An African monkey community*. (eds McGraw WS, Zuberbühler K, Noë R) Cambridge Univ. Press, Cambridge.