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# Chapter 1
# Meaning in the Wild

## *1.1 A snake encounter in Uganda*

In the heart of the Sonso forest, in Uganda, a group of primatologists is following a group of chimpanzees. For both sides, this is a routine occurrence. This group of chimpanzees has long been 'habituated', which means that they tolerate the presence of these human onlookers. The human scientists know the chimpanzees. They even know them by name: it is customary in studies of apes to give them proper names so as to keep track of who is who. But the chimpanzees know the humans too: while these may do their best to keep their distances and avoid any disruption, their presence never goes unnoticed, and any newcomer is discretely but intensely scrutinized by the elders.

Suddenly, while most of the chimpanzees are away, the humans hear a soft call: *hoo… hoo… hoo…* . It is produced by a chimpanzee, but there is no other chimpanzee in the immediate vicinity. Rather, his eyegaze goes back and forth between the field assistant, Sam, and the ground. It may have been hard to discern, but when one looks more closely, the reason becomes apparent: a snake is crawling. And it looks like the chimpanzee is trying to warn Sam: *hoo* is a snake alarm call, and the chimpanzee's eyegaze movement between Sam and the snake suggests that Sam was the intended audience.[4]

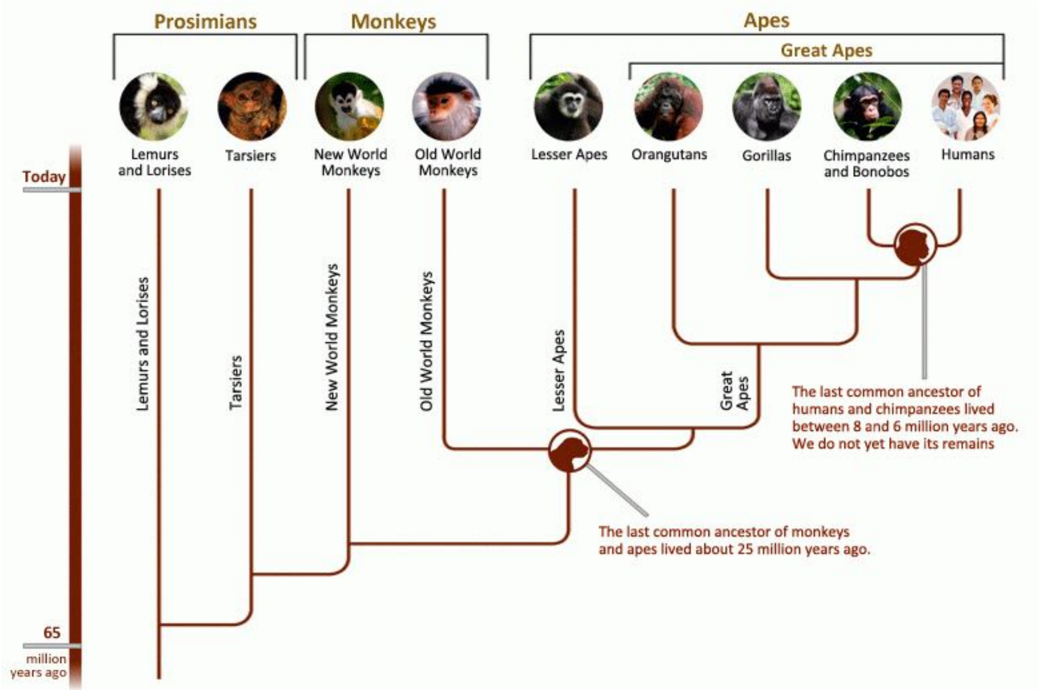
This real life anecdote raises fascinating questions about the relationship between the chimpanzees and the humans who study them. The primatologists do their best to avoid interacting with their primate cousins: the goal is to observe, not disrupt, and primatologists do their best to be as transparent as possible to the apes. But could it still be that some chimpanzees treat some humans as their friends? We do not quite know. In fact, the precise nature of the relationship is still a mystery.

But this anecdote also highlights a remarkable fact about ape communication: chimpanzees have signals that convey information about threats, and can be used intentionally, as illustrated here by the chimpanzee's eyegaze going back and forth between the field assistant and the ground, possibly to check that the snake has indeed been spotted. Still, an anecdote is just an anecdote, and short of systematic studies we will never know for sure what happened in the chimpanzee's mind on that particular day. To really understand how primate communication works, we need to harness the tools of science: systematic observations, field experiments, and precise theories. As it turns out, we humans are currently limited in our understanding of chimpanzee calls, possibly because they have social implications that escape us. Important headway was recently made in the understanding of ape gestures. But the most decisive progress was made when primatologists studied in detail the meaning of monkey calls (around the early 1980's).

## *1.2 Our primate cousins*

Before we plunge into monkey calls, we should pause to consider the primate family tree. Humans and chimpanzees have a common ancestor that lived between 6 and 7 million years ago. That's a long time. As a point of comparison, all current humans have a common ancestor that lived a few hundred thousand years ago. Bonobos are relatively close cousins of chimpanzees, and both species are equally closely related to us. Further cousins (more remote ones) are gorillas, orangutans and gibbons. All are apes, and like us they lack a tail. Monkeys have one, but they are more distant in our 'family' tree. To find a common ancestor between us and African and Asian monkeys (called 'Old World monkeys'), we need to go rather far back in time, 20-30 million years ago. And to find a common ancestor with American monkeys (called 'New World monkeys'), we need to go back 30-40 million years ago.

**Fig. 1.2.1** The primate family tree




*Credits:* Human Origins Program, NMNH, Smithsonian Institution
https://humanorigins.si.edu/evidence/genetics

How do we know all this? you might ask. The answer is: through DNA analysis. Parents pass their DNA to their off-spring, but the DNA isn't transmitted without modifications (called 'mutations'): occasional random 'errors' are made in the copying process, as when monks in the Middle Ages copied manuscripts by hand but made small errors in the process.[5] The more mutations have accumulated, the more distant the original copy. Furthermore, once a mutation has occurred, it will typically be inherited by later copies. So, by studying which of these mutations are shared among individuals or species, we can reconstruct their family tree.

### *1.3 Semantics: Vervet and Diana calls*

Among primatologists interested in communication, the Vervet monkeys of Africa are real stars: it was by studying their calls that three pioneers, Robert Seyfarth, Dorothy Cheney and Peter Marler showed in the early 1980's how sophisticated monkey calls can be.[6] But Vervets are not always as popular with the locals: unlike most monkeys we will discuss, they spend much time on the ground, and this means that they are very good at eating cultivators' crops. On a field visit to Uganda, we were anxiously awaiting our first encounter with the Vervets. Our field assistant asked a peasant where they could be found. Helpful indications were provided, with a suggestion that we eat the Vervets for dinner (it was made in jest: monkeys and apes are strictly protected from poaching in Uganda).

So why did the Vervets, who are not especially popular with the locals, become linguistic stars? Because they established the existence of a primate semantics: they have several calls, including three of which are respectively associated with raptors, leopards, and snakes. This association can be ascertained by carefully observing the situations in which the calls are produced. But how do we know that the calls are not just physiological reactions, devoid of any informational content? To establish this point, we must show that Vervets understand the content of these calls, and thus display the appropriate reaction when they hear them. So the first thing to do is to observe how Vervets react when they hear, say, a raptor alarm call. But things aren't so easy: many things happen simultaneously in the forest, and when a Vervet produces an alarm call, it may be hard to determine whether other Vervets are reacting to the call, or to what triggered it (the raptor), or possibly to something unrelated. To really understand what is going on, primatologists perform field experiments: they hide loudspeakers in trees and they play back alarm calls in the absence of any real threat. In this way, they can determine whether the calls can convey information on their own, independently of any disturbance in the forest.

The results of Seyfarth, Cheney and Marler's experiments were remarkable. The Vervets typically reacted appropriately. Not only this: their reactions suggested that they took into account both the informational content of the calls and their own situation to display the most appropriate reaction. In all cases, a Vervet that heard a snake alarm call tended to look down (what else would *you* do if you were told that there's a snake around?). By contrast, a Vervet that heard a leopard alarm call while on the ground didn't look down, but rather ran for cover or looked up (as leopards can climb on trees). But looking down was a useful reaction if the Vervet heard the call while in a tree, since the leopard could be coming from the ground, and this reaction was indeed found. Similarly, a Vervet that heard an eagle alarm call looked down more often when the Vervet was in a tree (as the eagle could be down below) than on the ground.

These results show two things. First, alarm calls convey specific information to the Vervets: not only do they produce them in some situations but not in others; they also understand the calls of others (including if these 'others' turn out to be facetious primatologists who, in the interest of science, have hidden loudspeakers in the trees). In other words, Vervet calls have a semantics. Second, Vervet calls genuinely seem to convey information about the world, rather than about the best reaction to display. One could imagine that calls are tantamount to orders, such as *run for cover* or *climb up*. But this is unlikely, since Vervets react to the same call in different ways depending on where they are in the tree: they don't look down when hearing a leopard call while on the ground, but they do look down if they are in a tree.

In order to drive home the point that there is a kind of equivalence in monkey minds between a raptor alarm call and genuine raptor presence, a beautiful experiment was performed by Klaus Zuberbühler, Dorothy Cheney and Robert Seyfarth in a different species, the Diana monkeys – distant cousins of the Vervets (they share a common ancestor approximately 7.5 million years ago).[7] There are three sub-experiment, which each involved two sounds played through a loudspeaker at times t and t+5 minutes. The second sound was always an eagle shriek, but the first sound differed across experiment. The goal was to determine whether the second sound produced new information that licensed an alarm or not.

| | | |
|---|---|---|
| 1st experiment: | **Eagle shriek at t = 0**<br>Dianas produce eagle alarm calls! | Eagle shriek at t = 5 min<br>Dianas **don't** produce eagle alarm calls<br>(eagle presence is old information) |
| 2nd experiment: | **Diana eagle call at t = 0**<br>Dianas produce eagle alarm calls! | Eagle shriek at t = 5 min<br>Dianas **don't** produce eagle alarm calls<br>(eagle presence is old information) |
| 3rdexperiment: | **Diana leopard call at t = 0**<br>Dianas produce leopard alarm calls! | Eagle shriek at t = 5 min<br>Diana **do** produce eagle alarm calls!<br>(eagle presence is new information) |

In an initial experiment, the primatologists started by playing back to the Dianas some eagle shrieks. Understandably alarmed, the male Dianas produced eagle calls at a high rate. Five minutes later, eagle shrieks were played again. The Dianas' reaction was muted – possibly because they already knew of eagle presence and had already warned the surrounding monkeys. This much is rather unsurprising.

In a second experiment, the shrieks played in the first one were replaced with Diana eagle alarm calls. Here too, the target individuals were alarmed, and responded with their own eagle alarm calls. But five minutes later, the primatologists played back eagle shrieks (rather than Diana calls), as they had in the first experiment. In that initial experiment, the monkeys were hearing the same type of sound for a second time, and thus it was unsurprising that they failed to react much. In the new version of the experiment, this wasn't the case: Diana eagle calls sound very different from eagle shrieks. But the Dianas' reaction to the shrieks was still muted, as if they had already known, thanks to the Diana eagle alarm calls, that there was an eagle around. As a result, hearing eagle shrieks didn't convey any new information. In other words, it seemed to be the conceptual equivalence between eagle presence and a Diana eagle alarm call that was responsible for this behavior.

Going one step further, the primatologists reasoned that if the initial Diana eagle call was replaced with a Diana leopard call, the reaction when hearing eagle shrieks should be anything but muted. This made sense because in that case the eagle shrieks conveyed entirely new information. The prediction was borne out in a third experiment: having heard a leopard alarm call rather than an eagle alarm call, the Dianas reacted with high call rates when they heard eagle shrieks five minutes later.

At this point, you might wonder how the monkeys learn what these calls mean. This question too can arise in any semantic investigation: once we know how the adults behave, we may want to understand how kids learn that behavior. With human language, nobody would think that we are born with a knowledge of what *car* or *dog* mean, but the situation is different with non-human primates. For starters, the form of their calls seems to be largely innate (i.e. genetically inherited): monkeys of the same species that were raised in entirely different groups usually have the same calls. Not only this, but these calls also seem to have the same meanings. In addition, hybrids born to parents from different subspecies have calls that are determined by their genetic heritage rather than by the environment in which they are raised: which calls they have does not seem to be much affected by which species they grow up with, and this highlights the plausibility of a genetic explanation. Things get even more surprising. In several of the monkey species we'll be discussing, males have different calls from females – they are louder, involve different sounds, and have different meanings as well. But juvenile males have female calls, and it's only around puberty that they start calling like males. How this happens in monkeys is still a bit of a mystery.

Still, we know something about call acquisition in Vervets. Seyfarth, Cheney and Marler analyzed the situations in which infants and juveniles used raptor calls, and they found something interesting. Even infants didn't use raptor calls in situations involving mammals. On the other hand, they called 'raptor' in all sorts of situations that involved non-threatening birds. Juveniles were more discriminating than infants, and adults only used raptor calls for predators that genuinely pose a threat. Is it that Vervet children have a different meaning for the raptor call than adults do? Or is it that for children and adults alike, the raptor call has a general meaning, akin to *Bird!*, but that children haven't yet learned that it's not worth calling attention to something that's not a threat? We don't know yet.

Much linguistic knowledge seems to be innate in primates: this is what explains the similarities among calls of socially unrelated groups (and also the calling behavior of hybrids). But one shouldn't conclude that *everything* about monkey calls is innate. There are definitely some examples of variation. Dianas and Vervets have another cousin species, the Campbell's monkeys, which are a bit closer to the Dianas than to the Vervets (the Dianas and Campbell's share a common ancestor approximately 6 millions years ago). Diana and Campbell's males have very different calls, but the Campbell's female calls are rather close to the Diana female calls, suggesting that calls can be preserved over millions of years (we will revisit this issue at the end of this chapter). But for all this biological determinism, Campbell's female calls were shown to be subtly different from one individual to the next. A genetic explanation would lead one to expect that call proximity reflects genetic relatedness: family members should thus talk in similar ways But this is not what was found when a group of captive (i.e. non-wild) monkeys were investigated in France: just like human children tend to talk like their friends, so similarly Campbell females were acoustically closer to their friends than to their family members.[8]

A more radical case of variation was found as well. In the same group of captive Campbell's monkeys, the females apparently created a new call, never heard in the wild: it was specifically used to warn of unfamiliar or unpopular humans, such as… the local veterinarian.[9] This finding should be taken with caution, as it is difficult to ascertain that a call is never used in the wild. Still, this case of linguistic innovation isn't isolated. In chimpanzees (who are much more closely related to us than to Campbells), some captive groups 'invented' a call that primatologists called the ‘Bronx cheer’ (or 'raspberry', or ‘splutter’). It was specifically produced when the chimpanzees needed to capture the attention of an inattentive human; and the call seemed to be produced intentionally, rather than as an automatic reaction to the presence of a threat, or of food, for that matter.[10]

### *1.4 Elusive syntax: Titi calls*

Stepping back, it seems clear that primate calls have meanings, just like words do (although words have… very different meanings, obviously). But there is more to language than individual words: from *Robin, loves* and *Casey*, we can form *Robin loves Casey* as well as *Casey loves Robin*. Not any order goes: *Loves Robin Casey* is not an English sentence: English has a syntax, i.e. a set of rules that define what is and what isn't a possible sentence. Furthermore, new meanings can be obtained from these combinations: the meaning of the whole *Robin loves Casey* is derived from the meaning of its parts, but the combination isn't trivial - in particular, it cannot be analyzed as a succession of utterances meaning: *There is someone named Robin. There is some loving relation. There is someone named Casey.* And of course different words orders would yield different meanings: it may be that *Robin loves Casey* even though the sentence *Casey loves Robin* is, alas, false. Do monkey calls have a comparable syntax?

The tiny Titi monkeys of Brazil initially suggested a positive answer. They are endearing little fellows. They mate for life, and entwine their tails to strengthen their couple's bond. They 'sing' duets together (possibly to mark their territory), and produce soft alarm calls that sound like bird chirps. But their life isn't easy: they are eaten by cat-like predators, and by eagles, and by some more famous monkeys, the Capuchins – notoriously smart primates that can eat meat.

Now the extraordinary thing is that with just two of their calls rearranged in different ways, the A- and the B-calls, the Titis encode information about the type of predator that's threatening them, and about its location. A beautiful field experiment was devised by Cristiane Cäsar and colleagues to demonstrate this.[11] This time the primatologists didn't hide loudspeakers in the forest; taking things a step further, they hid model predators, as life-like as possible: a model raptor, and a model cat. And they hid them in two positions: on the ground, or in the canopy (high in the trees).

When primatologists and then linguists inspected the results, they were flabbergasted: by re-arranging the calls in various ways, the Titi sequences encoded information about which kind of predator they saw, and where it was located. The results are illustrated Fig. 1.4.1, where each line represents the first 30 calls emitted by the Titis in the field experiment (any longer sequence just repeats the last calls).

**Fig. 1.4.1** Titi call sequences encode information about predator type and predator location

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Raptor in canopy** | 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 | 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 | 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 | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A |
| | A | A | A | A | A | A | A | A | A | O | O | A | O | A | A | A | A | A | O | A | A | A | A | A | A | A | A | A | A | A |
| **Raptor on ground** | 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 |
| | A | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | 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 |
| | 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 | A | A | A | A | A | A | A | A | A | A | A | A | B | B | A | A | A | B | A | A | A | A | B | B | B | B | B | A | B |
| | A | A | A | A | B | A | A | A | A | A | A | A | A | A | A | A | A | A | A | C | A | C | A | A | A | B | B | B | B | B |
| | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | B | B | B | B | B | B | B | A | A | A | B | B |
| **Cat on ground** | 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 |
| | 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 |
| | 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 |
| | 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 |
| | 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 canopy** | 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 |
| | 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 |
| | 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 |
| | 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 |
| | A | A | A | B | B | A | A | A | A | B | B | B | A | A | A | A | B | B | B | A | A | B | A | A | A | B | A | A | 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 |

Each line represents the series of (the first 30) Titi calls produced in reaction to the presence of a model predator (A-calls (dark gray), B-calls (light gray), and additional types without color: O, C, and ? in unclear cases).

*Credits:* Cristiane Cäsar. Original figure (redrawn and modified here) from: Cäsar, Cristiane: 2012, *Anti-predator Behaviour of Black-fronted Titi Monkeys (Callicebus nigrifrons)*, PhD dissertation, University of St Andrews. A correction to one call transcription is due to Mélissa Berthet.

Setting aside some extraneous calls (labeled C and O), the four blocks corresponding to the four experiments can be visually distinguished from each other rather easily. For a raptor in the canopy, a long series of A-calls. For a raptor on the ground, A-calls followed by B-calls. For a cat on the ground, a long series of B-calls. And for a cat in the canopy, a single A-call followed by B-calls.

Have we discovered syntax in monkeys? It sure doesn't look like human syntax because of the numerous repetitions: humans don't go around saying things like *Robin Robin Robin Robin loves loves loves Casey Casey Casey Casey Casey Casey*. But maybe we shouldn't hold the repetitions against the Titis: when your interlocutors are far away and it's important that you be heard, it might make sense to repeat yourself quite a bit (if your airplane must make an emergency landing, it's likely the pilot won't just say *Brace!* once, but rather *Brace! Brace! Brace!*…). So maybe we should abstract away from the repetitions, writing $A^+$ for any number of repetitions of $A$, and $B^+$ for any number of repetitions of $B$. With this notational trick, the Titi sentences start looking more orderly: $A^+$ means 'there is a raptor up', $A^+B^+$ means 'there is a raptor down', $B^+$ means 'there is a cat down', and $AB^+$ means 'there is a cat up'. The challenge for the primate linguist is to understand how these meanings come about.

Upon closer inspection, however, the prospects for a *bona fide* syntax appear bleak. The main problem is that these sequences are fairly slow, and due to the repetitions it would take a really long time to know whether you are hearing a 'raptor up' ($A^+$) or a 'raptor down'

($A^+B^+$) sequence. The unfortunate Titis would often have to wait for about 15 seconds to know whether the threat is coming from above or from below. If you are a Titi, the stakes couldn't be higher: understanding the calls quickly enough will determine whether you'll end up as somebody else's lunch.

So it's likely that the Titis don't interpret sequences as wholes. Instead, researchers have explored an alternative hypothesis: each call is a complete linguistic unit, a sentence if you will, and it provides information about the nature of the threat at the precise time at which the call is produced. But then what are the meanings of the A- and B-calls?[12]

At this point, we need to go beyond the beautiful field experiment we started out with, and observe some natural situations. The first thing to notice is that the B-call is used in extraordinarily diverse contexts: when there is a predator, when there is a ground mammal that isn't a predator, when the Titis are feeding, etc. Since these situations have so little in common, it makes sense to take the B-call to convey something very broad, such as: *something is happening* - a kind of completely general alert call.

The remaining challenge, then, is to discover the meaning of the A-call. An observation gave scientists a clue: it was regularly observed that when hearing an A-call, the Titis looked up. So it was hypothesized that the A-call means something like: *there is a serious threat up*. Both parts – *serious* and *up* – are important, as we will now see.

Let's go back to the $A^+$ sequence produced in 'raptor in the canopy' situation. It is certainly used to signal that there is a serious threat up in these situations, so the repeated *A* call makes sense. Furthermore, the model raptor is sure to stay put for as long as the primatologist desires. As long as the threat is present, the A-call can be produced, hence the long A-sequences we observe in the field experiment. In natural situations involving real predators, different patterns are found. For a flying raptor, we still find a sequence of A-calls, but it is much shorter: as soon as the raptor has flown away, there is no reason to keep calling anymore. When the raptor is perched, and potentially in a hunting position, the sequences are much longer.

What about the $A^+B^+$ sequences we find in 'raptor on the ground' situations? Well, the main idea is that raptors don't usually attack by crawling but by flying. This might explain why the Titis signal a serious threat up, hence the repeated A-calls at the beginning of the sequence: a raptor that's on the ground would probably attack by flying, and thus the threat would usually come from above. In addition, if a raptor stays on the ground for a while, chances are that it isn't in a hunting position; or it might also be that this just isn't a normal position for a raptor to stay in (unlike a perched position in a tree). Either way, after a while the Titi might decide that the threat isn't so serious, and thus the 'serious threat up' isn't licensed any longer. This explains why the sequence transitions to a B-call, which just says that there is something to pay attention to.

In 'cat on the ground' situations, the Titis don't have a choice, since it would be misleading to announce a 'serious threat up' by way of an A-call. So only the B-call can be used. The last case to be explained is the 'cat in the canopy' sequence, which in these data involves a single A-call followed by B-calls: $AB^+$. The initial A-call is unsurprising because there is indeed a serious threat up. But why don't we find the same pattern as in the 'raptor in the canopy' situations, with a series of A-calls? One (somewhat speculative) possibility is that the threats involved are different. A raptor in a tree likely presents a danger as long as it stays there. But for monkeys, cats are thought to be far less dangerous once they have been detected, as it is easy for the monkeys to climb in places that are hard to reach. In fact, in a different environment (African rather than South America), it was shown that leopards tend to abandon the hunt once they have been detected by monkeys. So while the cat in the canopy might initially be a *serious* threat, after its presence has been announced, it might become a more innocuous event. Announcing a serious threat would no longer be correct, and the A-call stops being appropriate, hence the appearance of the B-call.[13]

Titis teach us an important lesson: not everything that looks like syntax is syntax. To understand Titi call sequences, we did without any Titi grammar, of the kind needed to analyze *Robin loves Casey* or *Casey loves Robin*. All we needed were very simple call meanings, combined with plausible assumptions about the evolution of the threats in different situations.

This lesson has broader significance: primates have sophisticated communication systems, but so far there are no clear cases of a complex syntax. Interestingly, birdsongs are different: notes can be combined according to constrained and sophisticated rules. But as things stand, there is no evidence that these different combinations do anything but advertise the caller's quality, for instance to potential mates. In other words, there is no counterpart of our *Robin loves Casey* vs. *Casey loves Robin* example: human language remains one of a kind in this respect as in many others.

### *1.5 Pragmatics: the Informativity Principle*

If you were hoping for extraordinary linguistic feats by monkeys, Titi calls might have come as a disappointment: they seemed to promise some beautiful primate syntax, and all I did was convince you that far simpler hypotheses can explain the findings. But if we dig deeper, the Titis can tell us something quite extraordinary about monkey abilities, and about the difference between semantics and pragmatics.

To introduce the phenomenon, it is best to start from human language. If I tell you that *it is possible that Russia influenced the 2016 election*, you will normally infer that I don't take this to be a certainty, because if so I should have said: *it is certain that Russian influenced the 2016 election*. Now you could think that this is because *possible* means something like *conceivable but not certain*. But this wouldn't be quite correct. The reason is that I can say without contradicting myself: *It is possible, and in fact even certain, that Russia influenced the 2016 election*. Linguists have come up with a better analysis: *possible* competes with *certain*. On the assumption that *possible* means something like *there's at least a possibility*, *certain* is more informative. So if the speaker is cooperative and thus chooses the most informative sentence available, we can infer from the use of *possible* that *certain* wasn't open, presumably because it was overly strong – hence the *possible but not certain* inference we get in the Russia-related sentence.

This is a typical example of pragmatic reasoning (and an example of what the philosopher Paul Grice called an 'implicature'): the literal meaning of the words is enriched by reasoning on the speaker's motivations. In this way we get the inference we wanted: *possible* implies *not certain*, but this isn't due to a hard-wired ('semantic') component of the meaning of *possible*. Rather, it is just due to a plausible reasoning about the speaker's behavior (and for this reason, it is no contradiction to say *possible and even certain*). The specific reasoning I outlined is based on what is called the 'Informativity Principle', which mandates that speakers should be as informative as possible. This principle makes its effects felt in numerous other examples. If I ask you how you found a movie we just saw, and you tell me that *it was nice,* I'll have reason to think that you didn't quite love it, because if so you should have said something stronger, such as: *It was great!* (we will revisit the Informativity Principle in detail in Chapter 10).

Remarkably, Titis seem to have a version of the Informativity Principle. Let's think again about the data we just discussed. The B-call appears in all sorts of contexts, and thus we took it to have a really broad meaning, such as: *something is happening*. We gave the A-call a more specific meaning (*there is a serious threat up*), which did a pretty good job of explaining its distribution. But we didn't ask a simpler question: why isn't the B-call used all over the place? Given its extraordinarily general meaning, it should be true whenever something is happening

– including when there is a raptor that's about to attack! Now you might wonder: Why on earth would the Titis use a B-call in a raptor situation, when they have a perfectly appropriate A-call that provides much more useful information? And I agree, that would be strange. But this is just another way of saying that *the Titis seem to obey a version of the Informativity Principle*: if they can use something more specific than the completely general B-call, they do so.

Now we can't conclude from this that the *reason* the Titis do such a thing is that they are trying to be cooperative with their audience (e.g. along the lines of the following reasoning: 'I could use A, and also B, but my interlocutor will acquire more useful beliefs if I say A, so that's what I am going to say'). This would require an ability to represent other animals' beliefs, or in other words a theory of other minds, something that researchers are not necessarily ready to ascribe to monkeys (although there is some evidence for it in apes, as we will soon see). But the Titis could still have a kind of instinct that tells them to use the most specific call they have, thus obeying the Informativity Principle without a detour through a reasoning on their interlocutors' minds.

While it is still the object of debates, the Informativity Principle seems useful to analyze the calls of further primates, including ones (from Africa) that bear little relation to the South American Titis. Often one finds a fairly general call, and a specific raptor call. But one almost never finds the general call used in raptor situations; this might well be because all these monkeys obey the Informativity Principle. We will now see that this principle might also offer the key to the remarkable call system of a very different species, the African Campbell's monkeys.

### *1.6 Putting it all together: Campbell's calls*

While Vervets were stars of primate communication in the 1980's, in recent years they were eclipsed by Campbell's monkeys, studied in particular by Karim Ouattara and colleagues.[14] Campbell's calls offer a case study in primate linguistics, with a tiny bit of syntax, some semantics and some pragmatics combined in one system.

I briefly mentioned above the Campbell's females, who talk with the mannerisms of their friends rather than of their family. But males are no less interesting. In the forest, a resident male warns his group – a harem of females, and juveniles – of impending threats. His calls are loud, and invariably given by the same individual, as there is only one resident male per group. This makes male calls much easier to study than female calls, as the latter are much softer, and often given by an entire group.

Male Campbell's calls are remarkable for several reasons. First, they include a non-predation call, *boom*, which is low in frequency, loud, and heard far away in the forest. Primatologists aren't sure of the precise meaning of *boom*, but it is never used in the presence of predators, and seems to function to establish group coherence and possibly to defend territory ('I am here!'). Remarkably, *boom* usually appears at the beginning of call sequences, as a single pair (*boom boom*). So it seems that the Campbell's have a syntactic rule governing the use of *boom* – and this might be more robust than our initial impression that Titis have syntax! (Full disclosure: I try to remain cautious on this one, because besides *boom*, little order could be found in Campbell's call sequences, either because there is none, or because we weren't smart enough to detect it.).

The second remarkable thing is that some Campbell's calls have an internal structure. This is a common occurrence in human languages: from *inform* you can derive *informative*, and from that *informativity*, a word you read a few paragraphs back ('Informativity Principle'). Here we obtained two new words by successfully adding the suffix *-ative* and then the suffix *-ity*. Linguists call this morphology, the rules by which words are made. But morphology *in monkeys*? That's more surprising. And yet Campbell's monkeys seem to have a suffix, namely *-oo*. Just like male Dianas, Campbell's have a call warning of eagle presence: *hok*. But they also have a call *hok-oo*, warning of less serious non-ground (e.g. aerial or arboreal) threats. For instance, they use *hok-oo* when they encounter other monkey groups (Campbells, just like Dianas, live in trees, so the encounters will usually take place in the trees as well). *-oo* genuinely seems to function like a suffix: it is added to a word to form a new word with a related meaning. From *green* you can form *green-ish* ('kind of green'), from *blue* you can form *blue-ish* ('kind of blue'), and *-ish* makes the same contribution in both cases. Something similar is found in Campbell's, and *-oo* is even reminiscent of *-ish: hok* is used for serious non-ground threats, and *hok-oo* is used for attenuated versions, less serious non-ground threats.

But couldn't it just be an accident that *hok* and *hok-oo* have a part in common? In English, the adjective *irate* (meaning 'very angry') is made of two syllables, and each syllable has an independent meaning (*I* = the first person pronoun, *rate* = the verb), but that's a pure accident – nobody would dream of analyzing *irate* as being made of *I+rate*, since to be irate has nothing to do with any kind of rating! While we can't completely exclude that *hok-oo* presents a similar accident, two facts militate against this conclusion. For starters, there is a very brief pause between *hok* and *-oo* in *hok-oo,* as if the call acoustics were telling us that it's genuinely made of two parts (not that this is a requirement to be a suffix, mind you – you don't have such pauses in the English examples I discussed; but if we want to argue that *hok-oo* has two parts, finding a tiny pause between them is still helpful).

But there is more. In the case of *green - greenish*, the main argument for an analysis with a suffix is that *ish* can be added to other adjectives, such as *blue*. As it turns out, *hok* is not alone in taking *-oo* as a suffix. There is another call, *krak,* which was initially analyzed as a leopard alarm call. And from *krak+oo*, Campbell's monkeys form *krak-oo*; and it too seems to be an attenuated call of sorts, used for all kinds of alerts, not just predator-related ones (we'll refine this point below).

So this is the language of Campbell's monkeys: *boom* is used for situations of non-predation and appears as a pair, at the beginning of sentences. *Hok* is used for serious non-ground threats (eagle-related threats), *hok-oo* for all sorts of non-ground alerts. *Krak-oo* is used even more generally, for all kinds of alerts, whether ground or non-ground, while *krak* is used for serious ground threats (leopards).

I have simplified things a bit, however. I described the Campbell's call system as it is found in the Tai forest of Ivory Coast. But Campbell's monkeys were also studied in a different site, on Tiwai island in Sierra Leone. And they had another surprise in store for the primatologists (Kate Arnold, Sumir Keenan and colleagues): while most of the calls had the same form and meaning as in the Tai forest, there was one striking exception. *Krak*, which was used as a leopard alert in the Tai forest, appeared to be used as a completely general alarm call on Tiwai island. Most surprisingly, although Campbell's monkeys of the Tai forest almost never used *krak* for eagles (reserving this call for leopards), their cousins of Tiwai island produced lots of *kraks* when eagle presence was simulated. The rough meanings of Campbell's calls are thus the following (with a difference between Tai and Tiwai regarding *krak*):

(1) **Campbell's calls**
boom boom (only at the beginning of sequences): situations of non-predation
hok: eagle presence
hok-oo: non-ground alert
krak: (i) leopard presence (Tai); (ii) general alert (Tiwai)
krak-oo: general alert

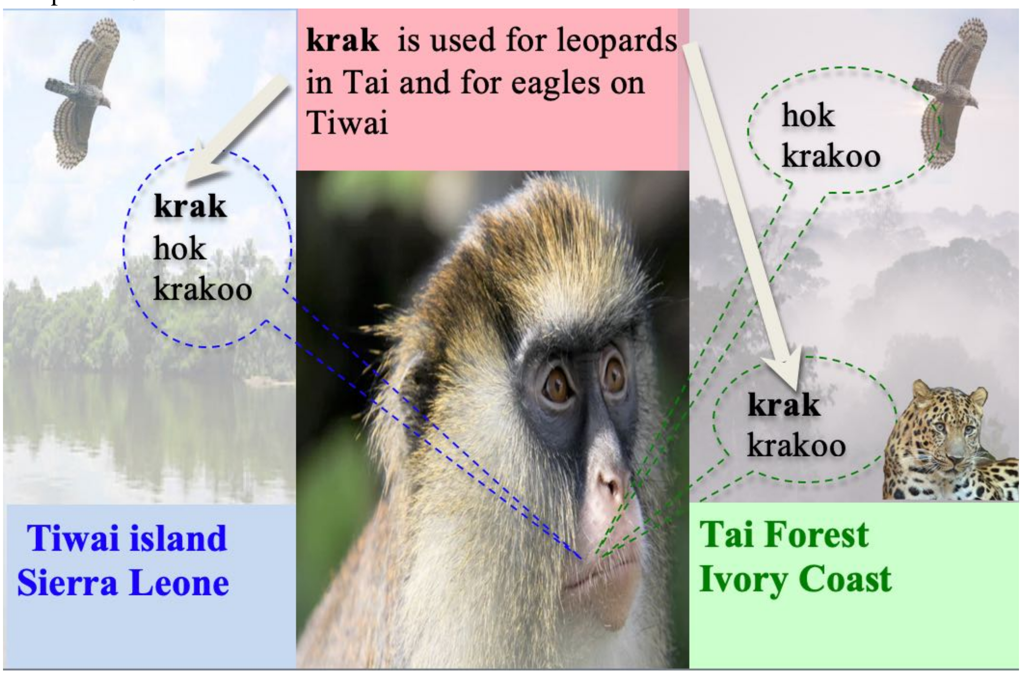
There is an interesting environmental difference between the Tai forest and Tiwai island. While Tai and Tiwai both have eagles, leopards haven't been seen on Tiwai island for dozens and dozens of years. Primate calls are thought to be largely innate. We saw an example of this when we discussed the use of the eagle call by infant Vervet monkeys: they know from the start that it should only be applied to birds. So what should we expect of Campbell's monkey calling behavior on Tiwai island? If the meaning of the *krak* call is innate, and if it genuinely warns of leopard presence, we would just expect it not be used on Tiwai island. But this isn't at all what primatologists found: the call was used all over the place, with a completely general meaning – so much so that on Tiwai *krak* and *krak-oo* seemed to have roughly the same meaning (whereas in the Tai forest, *krak* was primarily used to warn of leopard presence).

When linguists and primatologists analyzed these data, they couldn't rule out that there was a bit of dialectal variation across Campbell's monkey populations. The Irish writer George Bernard Shaw famously quipped that England and America are two countries divided by a common language, and that's in part because it's not *quite* the same language: for instance, *pants* is used to refer to trousers in the United States, but to underpants in Great Britain. Since we already saw that there is a bit of linguistic innovation in primates (as in the case of the chimpanzee 'Bronx cheer' made to humans), we couldn't exclude that at some point one group 'invented' a new meaning for *krak*.

But upon closer inspection, something else was puzzling about these calls, even just looking at their use in the Tai forest. *Hok* refers to serious non-ground threats, and *hok-oo* to an attenuated version of these threats. In the Tai forest, *krak* refers to serious ground threats, so by parity of reasoning, we could expect that *krak-oo* refers to attenuated ground threats. But the facts were different: in the Tai forest, *krak-oo* was used as a genuinely general call, for ground and non-ground threats alike.

In the end, then, we have two puzzles on our hands: why is there a difference in the meaning of *krak* between the Tai forest and Tiwai island? And focusing on Tai, how is the meaning of *krak-oo* derived from the meaning of *krak* and *-oo*? This is illustrated in the following figure (from which I have removed *hok-oo* for simplicity).

**Fig. 1.6.1** The puzzle of *krak*

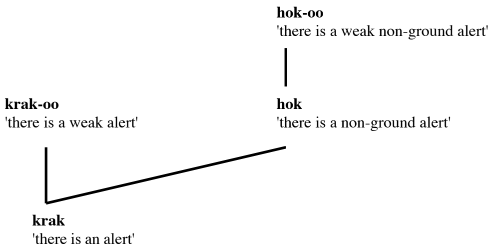



*Credits:* Author's figure, using: Campbell's monkey: © UR1/Dircom/JLB, with permission; leopard: Art G. from Willow Grove, PA, USA, https://commons.wikimedia.org/wiki/File:Amur_Leopard_(1970226951).jpg

Linguists devised a solution to solve both problems. It makes crucial use of the Informativity Principle. To start with, consider *hok* and *hok-oo*. The idea is that *hok* is used for non-ground (e.g. aerial) alarms, while *hok-oo* is used for non-serious aerial alarms. If we stopped here, the analysis would be wrong: *hok* is used for raptor alarms, not for other non-ground alarms. But the Informativity Principle comes to the rescue: *hok-oo* is more informative than *hok*, since if there is a *non-serious aerial alarm*, there is certainly an *aerial alarm*. By the Principle, if *hok* is produced, this is because the more informative call *hok-oo* couldn't be, so the alarm wasn't non-serious: it was a serious alarm!

In Fig. 1.6.2 below, I've put *hok-oo* above *hok* because the former more informative than the latter. The Informativity Principle tells us that *hok* can only be used when *hok-oo* can't, so if *hok* is used, there must be a serious aerial alarm.

**Fig. 1.6.2 Informativity relations among Campbell's calls**
*For two calls that are linked, 'higher' means 'more informative'*.[15]




When taking into the Informativity Principle, the contribution of *krak* is:
krak and not krak-oo and not hok
i.e. there is a serious, ground-related alert.

When we come to *krak*, things get more interesting. We take its literal meaning to be the one it has on Tiwai: *krak* is just a general alarm call. Since we want *-oo* to have the same effect when applied to *hok* and to *krak*, we have no choice but to say that *krak-oo* is used for non-serious alarms. Now let's go back to *krak*, taking into account the Informativity Principle. *Krak-oo* is of course more informative than *krak*: if there is a non-serious alarm, there is an alarm (this is the same reasoning we did for *hok-oo* and *hok*). But *hok* is also more informative than *krak*: if there is an aerial alarm, there is an alarm. So *krak* can only be used when these two competitors cannot be. In other words, it can only be used when there is an alarm, but it's *not* non-serious (so it's serious!), and it's *not* an aerial one (so it's ground-related!).

Putting everything together, *krak* can only be used when there is an alarm, and it is serious, and it is ground-related. Now put yourself in the shoes, or fur, of a Campbell's monkey of the Tai forest, where the main predators are eagles and leopards. What could a serious alarm that's ground-related refer to? Leopards, of course! We have derived the correct use of *krak*.

The only thing that remains to be explained is why *krak* doesn't have the same overall meaning on Tiwai island ('serious ground-related alarm'). Let's think about this a bit more. If there was such a meaning on Tiwai, it would be pretty useless, since there are no leopards and thus no serious ground threats on Tiwai. At this point, we must remember that the ground predator inference isn't hard-wired in the meaning of *krak*: it's the Informativity Principle that leads to this inference. So all we need to posit is that the enrichment of meaning due to the Informativity Principle doesn't take place if it gives rise to a useless result: monkeys aren't stupid.

In sum, Campbell's male calls have a semantics, and also a tiny bit of morphology, with a suffix *-oo* that can modify the meaning of *hok* and of *krak*. They might have a syntactic rule: *boom boom* comes as a pair at the beginning of sequences (although the rest of the syntax is… a mess). And a case can be made that they obey a pragmatic rule, the Informativity Principle, which mandates that the most informative calls should be used whenever possible. Campbell's monkeys thus offer a miniature system of what semantics (broadly construed) is all about.

### *1.7 Bilingualism in the wild*

Some of us know several languages – but these are languages used by our own species. Our primate cousins routinely understand the language of *other species*. Take the Diana monkeys. As we saw before, the males produce very different calls from the Campbell's males, with whom they share a common ancestor approximately 6.5 million years ago. But Campbell's and Dianas often live in the same trees, and thus they have much experience with each other's calls. And they have ample reason to understand the neighbors' calls, as these may warn of impending threats: bilingualism might be a matter of life and death.

And bilingualism there is. Diana monkeys understand Campbell's calls, down to the details.[16] Let us go back to the Tai forest, but turn our attention from the Campbells to the Dianas. Hiding once again a loudspeaker in the trees, we play back a series of Campbell's *krak* calls, which in this environment are indicative of leopards. The Dianas respond with their own calls appropriate for ground predators. If instead we play back a series of Cambpell's *hok* calls, the Dianas respond with their own eagle calls. Although the Dianas don't speak the Campbell's language, they clearly understand some of it.

But how detailed is their knowledge? It took us humans quite some time to understand the workings of *boom*, *krak, hok, krak-oo and hok-oo*. Are the Dianas more gifted polyglots? Take *booms*. When they appear in Campbell's call sequences, they are a sure sign that the situation is not one of predation. The Dianas themselves don't have *booms*. But remarkably, they understand their meaning. How do we know? As before, we play back to the Dianas some Campbell's leopard- and eagle-related sequences. But now we artificially add to them *boom boom* at the beginning. This time the Dianas stop responding in anything like the same way as before: they know that *boom* is a non-predation call. In fact, they know something more precise, namely that *boom* is indicative of non-predation *when it is produced by Campbells*. How could we tell? We wish to exclude the more mundane possibility that they know that whenever *boom* is produced, there is no predator around. To test this, we now play back a hybrid sequence made of a Campbell's *boom boom* followed by a Diana sequence warning of leopard or eagle presence. But now the Dianas react with alarm: they know that the *boom boom* pair doesn't belong in a Diana sequence, and they just ignore it. In other words, they interpret the Diana sequence without the extraneous Campbell's calls that were deviously added by the primatologists.

And it's not just that the Dianas understand the Campbells. The Campbells understand their Diana neighbors too. So much so, in fact, that primatologists sometimes use Diana calls to trigger Campbell's calls: the Campbell's immediately decode Diana call content and relay it with their own calls.

This kind of bilingualism might seem remarkable, but it is by no means exceptional. While our primate pride might suffer from this observation, some birds understand Diana monkey calls. Such is the case of the hornbill, a large, majestic bird with an impressive beak and a slow flight.[17] When you play back some Diana calls, it reacts with its own calls, but in a selective fashion: Diana eagle calls elicit a reaction, but Diana leopard calls don't. No wonder: eagles are a threat to hornbills, but leopard are not (they may climb on trees, but they can't fly). Hornbills thus respond as they should; but this is possible only because they understand the difference between Diana leopard and Diana eagle calls.

### *1.8 Call evolution*

In 1876, the Linguistic Society of Paris famously prohibited any further debates on language evolution because this topic had only produced the wildest of speculations. The situation has improved, but not as much as one would have hoped. Take this long-standing question: did human language originally start developing in sounds or in gestures? There have been endless debates, and a bit of progress, but the question is still considered fairly open among scientists (which doesn't prevent some of them from having strong opinions on this matter; it's just that different scientists have strong opinions that go in opposite directions). Given how distant monkeys are from us, any hope of connecting their calls to human language is of course even more remote.

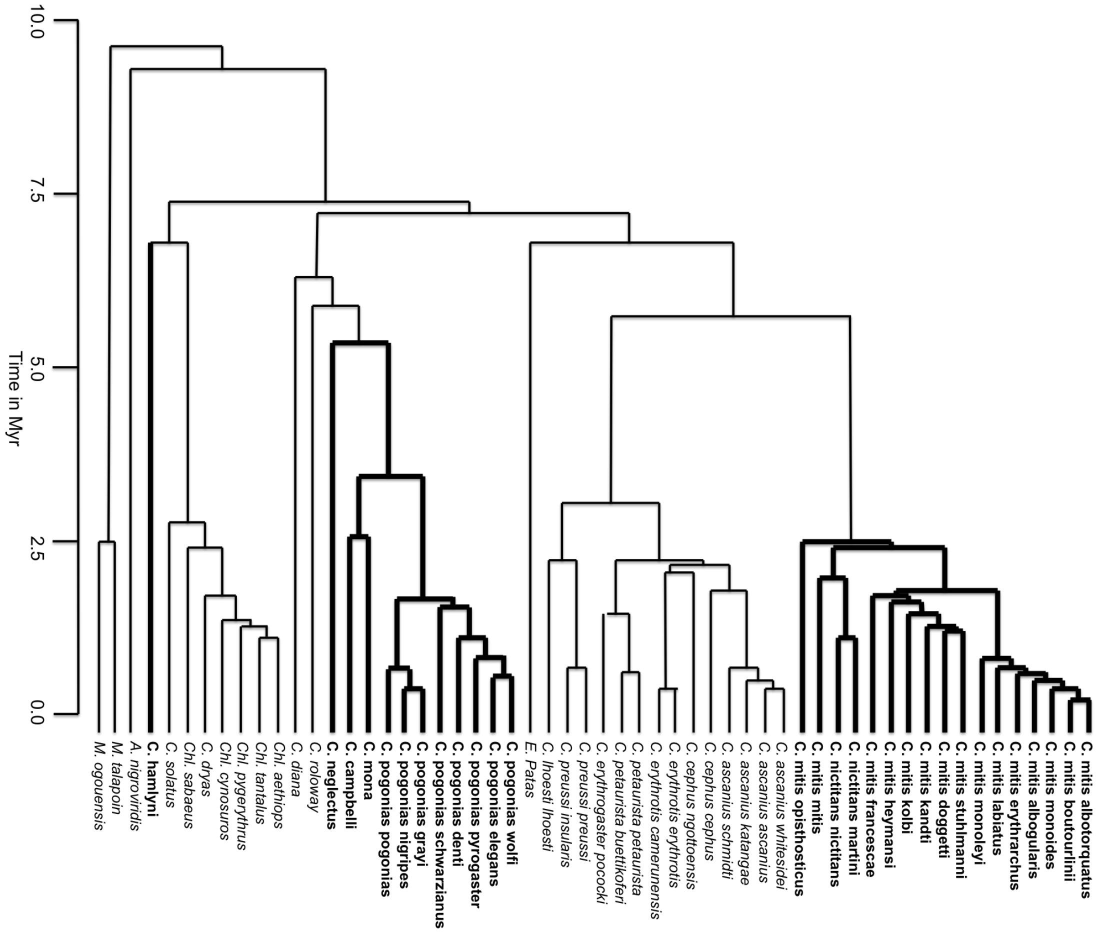
But there is a little scientific secret that even scientists have made insufficient use of: it is that the evolutionary history of some monkey calls can be reconstructed over millions of years. Think about it: in humans, the state of language three hundred thousand years ago is a very controversial topic, and one would be hard pressed to find a strong argument that a particular word already existed at the time with a particular meaning. But as we will now see, the situation is entirely different with Campbell's monkeys and their relatives.

**The story of *boom*.** Let's go back to the *boom* call, which may appear at the beginning of Campbell's male sequences and is a signal of non-predation. It's not hard to reconstruct its history over millions of years, and to conclude with great certainty that it was already present 2-3 million years ago.

*But you weren't there*, you might object, *so how could you know?* By combining two sources of information: DNA data, which help reconstruct the history of species, and the distribution of *booms* in today's monkey species. The key observation is that the Campbell's are not alone in having *booms*. True, their cousins, the Dianas, don't have them – which made it all the more remarkable that they still understand them. But many other members of the Diana and Campbell's family have *booms*. To get a glimpse of the situation, we start from 'family tree' obtained with DNA methods, and we plot which species do and which species do not have *booms*. We immediately find something remarkable: there are two subfamilies all of whose members have booms.[18]

In the family tree in Fig. 1.8.1, I have boldfaced current members of the Campbell's and Diana family that have booms (this entire family is called Cercopithecines). Species that have booms cluster around two coherent sub-families: one had a common ancestor 2.5 million years ago, the other had a common ancestor 5 million years ago. While it could be that these ancestors didn't have *booms* and these happened to appear independently several times, a more parsimonious and thus convincing theory is that both ancestors already had *booms*.

**Fig. 1.8.1** The evolutionary history of boom




'Family' tree of cercopithecines, the group that includes Campbell's monkeys and Diana monkeys, with boldfaced names for species that have *booms*. *C.* is short for *Cercopithecus,* the general family name, complemented with the full official Latin name of the relevant species. It seems very likely that the most common recent ancestor of the right-most boldfaced (= *mitis*) group (which lived about 2.5 million years ago) had *booms*, since all of its descendants do; and similarly for the most recent common ancestor of the boldfaced group in the middle (*C. pogonias*, *C. mona*, *C. campbelli*, *C. neglectus*).

*Credits:* L. Ravaux[19]

This method makes much sense if we think of calls as being part of monkey biology. Within our own primate lineage, the apes have in common the absence of a tail: humans, chimpanzees, gorillas and orangutans all share this property, unlike monkeys. We could of course imagine that the most recent common ancestor of the four groups had a tail, and that it was lost independently in several lineages. But a more parsimonious explanation is that the most recent common ancestor had no tail either (and this is indeed what evolutionary biologists think). The same reasoning carries over to *booms*.

Can we go further, and conclude that the most recent common ancestor of *all* the monkeys in the Cercopithecine family had *booms* as well? Here I'll have to say that we don't know. Maybe it did, and *booms* were lost in several subfamilies. The data are not overwhelming, because some subfamilies have booms while others don't. But if we limit our ambitions to 2.5-5 million years ago, some solid inferences can be drawn, because we find subfamilies whose members *all* have booms.

This is not an isolated case. Monkey calls are often preserved over millions of years, and thus shared among close or distant cousin species. In fact, calls are so well preserved that in the 1970's and 1980's, when DNA methods were not as easily accessible as they are today, call similarity was sometimes used *in lieu* of DNA to reconstruct the family relationship among monkey species. Strikingly, the results converged with those of DNA methods.[20] Now that we have the luxury of easy access to reliable DNA methods, we can turn the problem on its head: instead of using call similarity to reconstruct monkey evolutionary history, we start from well-established family relationships, and use them to reconstruct the evolution of monkey languages.

### *1.9 Ape communication: calls*

If monkeys have sophisticated communication systems, we might expect to find something even more remarkable in our closest cousins, the apes, especially the chimpanzees, bonobos, and gorillas. Unfortunately, their call systems aren't well understood yet, although there might soon be progress on that front. Still, two important discoveries were made about ape communication. First, unlike the species we have discussed up to this point, apes have sophisticated means of gestural communication. This difference makes sense. Campbell's monkeys and their close cousins usually live in trees, and thus a speaker and its audience have little chance of seeing each other: using predominantly vocal rather than visual signals is the thing to do. By contrast, chimpanzees, bonobos and gorillas spend much time on the ground, in visual contact with each other, so both vocal and gestural signals can be useful. There is a second difference as well. As I noted when I mentioned the Informativity Principle ('pick the most informative call possible!'), there is no clear evidence that monkeys can represent what other monkeys think, and for this reason it was hard to argue that monkeys try to be as informative as possible *in order* to be cooperative with their audience (a standard assumption for humans). But it is increasingly likely that apes do have a representation of what their audience knows.

The evidence comes from experiments conducted with chimpanzees and model snakes, conducted by Catherine Crockford and colleagues.[21] I started this chapter with the chimpanzee *hoo* alarm call, produced to warn of snake presence. The tantalizing possibility in this initial anecdote was that the intended audience was made of… a human. But in less extraordinary circumstances, it is made of other chimpanzees. In such cases, does the caller produce the call automatically, or does it adapt its calling behavior to what its audience knows? Automatic call production can't be ruled out for monkeys, but for chimpanzees it's unlikely to be the full story.

Think for a second about what you would do when your interlocutor is aware of a threat. Suppose you and I are walking together in the forest, and suddenly you see a snake, and it's obvious to you that I've seen it too – maybe because of my startled reaction. Will you then say: *Watch out, a snake!* Probably not, unless you think that I am really dense. That's another principle of pragmatics (call it the 'Economy Principle'): not only does one try to be as informative as possible; one also doesn't go around stating the obvious. On the other hand, if I didn't see the threat, warning me explicitly will be appropriate and (hopefully) called for. Finally, if somebody else warned of the snake's presence, you might or might not reiterate the warning depending on whether you think I am aware of the danger.

In other words, you won't just produce the warning automatically: you will adapt the signal to what you can infer of my state of knowledge. You can do this because you have a theory of other minds. In this case, chimpanzees seem to behave like us. The primatologists hide a model snake, and observe the target chimpanzee's reaction depending on what it could know about its intended audience – other chimpanzees. Sometimes these could not have seen the snake, nor heard a *hoo* call. If so, the target chimpanzee has no reason to believe that its audience knows anything about the danger, and it should produce lots of *hoos*. On the other hand, if the target chimpanzee can determine that its audience has seen the snake, far fewer *hoos* should be produced, as one doesn't go around stating the obvious. Finally, if the audience has heard some *hoo* calls, but it cannot be determined that they have *seen* the snake, an intermediate number of calls should be produced by the target chimpanzees. This three-way distinction is exactly what was found: chimpanzees, just like humans, take into account what their audience knows before saying something, and they don't go around stating the obvious: they go by the Economy Principle. That's one aspect of pragmatics that they seem to share with us.

Still, it is fair to say that the details of the chimpanzee call repertoire are not entirely understood yet. They have further calls besides *hoos* – they produce *grunts* and *barks* and *pants* in different situations, but the basic units as well as their meanings are still elusive.

### *1.10 Ape communication: gestures*

If ape calls are still a bit of a mystery, recent discoveries about gestures are revolutionizing our understanding of ape communication, thanks in particular to the work of Catherine Hobaiter, Richard Byrne and colleagues.[22] So much so that primatologists now have a kind of 'chimpanzee gesture dictionary' comprising at least 60 or 70 communicative gestures, which are found in socially unrelated groups and are likely to be innate.

**Gesture use:** The first thing to note is that ape gestures, just like *hoo*, are produced while taking into account the state of knowledge of the addressee. If you want to express your enthusiasm at a suggestion I made, you might say *Great!* or use the thumbs up gesture 👍. But if we are talking over the phone, you'll preferably use sound because you know I can't see you. Chimpanzees and bonobos do the same thing: they may use silent visual gestures when their audience is looking at them, but otherwise they preferably use calls (or contact gestures that can grab their audience's attention).

In fact, there is evidence that these gestures are used intentionally, to achieve a specific goal. Thus apes typically repeat a gesture until the outcome is satisfactory. Researchers showed that orangutans take it one step further. Faced with a human keeper that partly understands their gestural request, giving them only half of the desired food, they just repeat the same gesture, hoping that their dense interlocutor will finally get the message. But faced with a completely incompetent keeper that continually hands the wrong food, they give up and switch to a different gesture, one that might be more effective with their linguistically challenged interlocutor.[23]

**Pointing and iconicity:** Two things often come to mind when one thinks of gestures: pointing, and iconicity, which is the ability of a gesture to resemble what it denotes (as when you trace an imaginary path with your finger to tell your interlocutor which way to go). A striking anecdote suggests that some apes can master both. It involves a female chimpanzee of a zoo in the United Kingdom, who had had early exposure to humans. At the beginning, one sees the chimpanzee pointing (human-like, using the index) through a window at a visitors' bag – and to make sure that there is no ambiguity, the chimpanzee comes closer to the bag while continuing to point. The visitors take a bottle of soda out of the bag, and the chimpanzee makes a beckoning gesture to tell them to follow her, then points towards the bottle, then towards a small hole under the window: she wants the humans to pour the liquid so she can get her share. Utterly charmed, the visitors comply. Having quenched her thirst, the chimpanzee would now like to fill her stomach, hence a new pointing gesture towards the bag. It contains a banana, but clearly it won't go through the hole. So now the chimpanzee points her finger upwards, iconically tracing the imaginary path that the banana should follow: the humans are being instructed to send it over the glass wall. Charm doesn't quite do it this time, so the chimpanzee is content to ask for more soda ([**AV1.10.1** https://youtu.be/E7fua-nbpHc]).

There is a grain of general truth in this video. As in any anecdote, however, interpretation is difficult: How much early contact did this chimpanzee have with humans? Would other chimpanzees display similar abilities? Here the results are a bit conflicting. While this may come as a disappointment, a dog will likely understand your pointing gestures far better than a chimpanzee would. And this result was obtained experimentally: a group of dogs was compared to two groups of chimpanzees, one from a zoo in Germany, the other from a sanctuary in Uganda.[24] The animals were rewarded if they brought back an object that the experimenter had pointed at. Dogs succeeded above chance, chimpanzees just didn't. This is less surprising than it seems: dogs have been domesticated for at least 10,000 years, and thus they have had ample time to evolve with humans and to adapt to their communicative cues, unlike chimpanzees.

Other experiments specifically focused on captive chimpanzees' understanding of iconic gestures: a chimpanzee had to maneuver a complex apparatus to get some food, and the human experimenter produced an iconic gesture resembling the correct action, such as pushing something in or pulling something down. To assess the role of iconicity, arbitrary gestures (whose form didn't provide information on what to do) were tested as well. 4-year old children often succeeded at the task when seeing iconic but not arbitrary gestures. Chimpanzees were bad at the task in both cases (over time, they did make greater progress with iconic than with arbitrary gestures).[25]

But some results go in a different direction. The short of it is that apes reared by humans seem to routinely use pointing. Anecdotes are legion. The primatologist Robert Yerkes recounts a case in which a captive chimpanzee, Moos, had been ill and was refusing hard foods. Moos readily responded to a dental inspection by a caregiver, but the latter didn't detect anything wrong. “Satisfied with his examination he turned to leave the room, but Moos took hold of his coat, drew him back, and raising his upper lip with one hand pointed with a finger of the other hand to a spot on his upper jaw", where the caregiver found an erupting tooth – and was apparently "chagrined at having to be assisted in the diagnosis by the animal himself".[26] In one study, about half the chimpanzees that lived in zoos and research centers used pointing.[27]

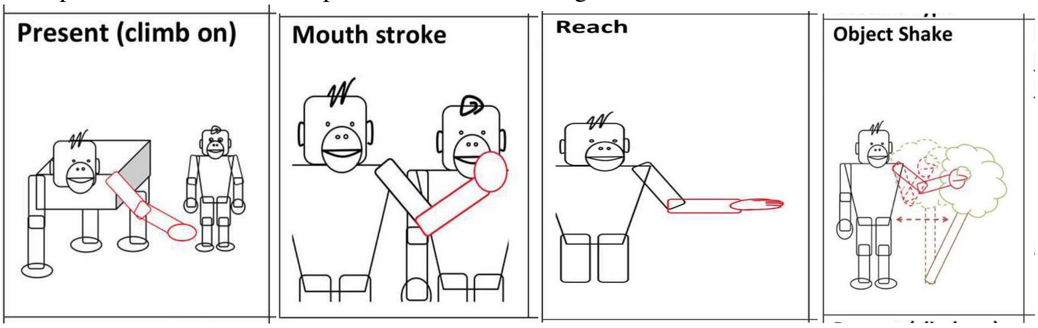
Still, these observations only assess how apes understand or use human gestures. A more relevant question is whether there are instances of pointing and iconicity in the natural gestures that apes use in the wild. As a first approximation, these are extremely rare, although not entirely absent. Some of the most striking examples involve bonobos, a more quiet and considerably more promiscuous species than chimpanzees: bonobos are known to go by the adage 'make love, not war', and to use sex with partners of both sexes to foster social bonds and relieve tension. One signal is a beckoning gesture towards a location where they wish to invite their interlocutor to have sex – a pointing gesture of sorts.[28] Another X-rated example pertains to bonobo females that wish to initiate mutual genital rubbing with another female. The signal involves foot pointing (with the heel or toe) towards the initiator's sexual swelling. The same goal can also be achieved through a less subtle cue: by way of hip movement, the initiator will pantomime the action that takes place during genital rubbing – an iconic gestures of sorts.[29]

Despite these advances, the status of pointing and iconicity in ape gestures remains a matter of debate. And more generally, we don't know much about the relation between ape gestures and human language. Still, ape gesture research has led to another fascinating finding: a large part of ape gestures are shared among ape species. Using the same kind of argument we developed in our little evolutionary history of *boom*, we can draw the conclusion that most ape gestures are millions of years old.

**Evolution of ape gestures:** Unsurprisingly in view of their close family relationship (they share a common ancestor approximately 2 million years ago), chimpanzees and bonobos have particularly similar gestures, despite the fact that they live in different areas. Not only do they have lots of gestures in common; their meanings are often related as well.[30] How do we know what the meanings are? At this point, we don't have sophisticated linguistic analyses to offer. But primatologists took advantage of the fact that these gestures are produced with a goal in mind: they listed outcomes that count as satisfactory because they put an end to the gesturing. These 'apparently satisfactory outcomes' can serve as a first approximation of gestural meanings. I don't think they are likely to correspond directly to the apes' mental representations of these meanings, but they are still a very useful way to approach them.

To start with a simple example, in bonobos and chimpanzees alike, a hand gesture directed at an infant (1st picture below) is a signal to climb on the gesturer. Similarly, a mouth stroke (2nd picture below) is in both species used as a signal that the gesturer wishes to acquire an object. A reaching gesture (3rd picture below) by a chimpanzee is primarily an indication that they want to acquire an object, whereas the same gesture used by a bonobo is an invitation to climb on them. In chimpanzees, shaking an object (4th picture below) is primarily a way to suggest to the addressee that they follow the gesturer. True to form, the bonobos primarily give this gesture a more sexual meaning, although sometimes the satisfactory outcome just involves grooming. So there are similarities and differences between the meanings that the two species assign to a given gesture type, but researchers have still been able to show that shared meanings are much more common than would be expected by chance.

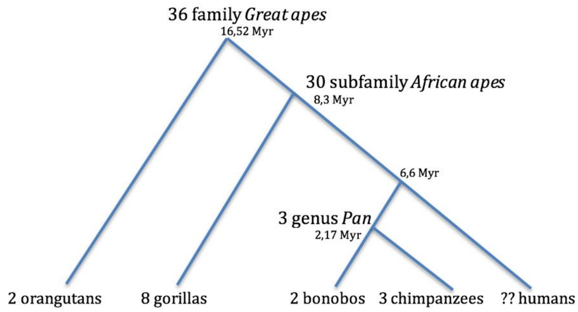
**Fig. 1.10.1** Examples of bonobo and chimpanzee communicative gestures




*Credits*: Catherine Hobaiter, Richard Byrne and colleagues, The Great Ape Dictionary, https://greatapedictionary.ac.uk/gesture-videos2/. University of St Andrews. Figures drawn by Kirsty E. Graham.

When it comes to form, shared gestures do not just occur in the bonobo and chimpanzee branch of the ape family tree: they are the norm among apes.[31] After a painstaking study of chimpanzee, bonobo, gorilla and orangutan gestures, primatologists concluded that 36 are typical of the entire ape family, from chimpanzees and bonobos to orangutans, while an additional 30 gestures are typical of the chimpanzee/bonobo/gorilla group. You can see this in the 'family tree' of apes that appears below: chimpanzees and bonobos are our closest cousins, then come gorillas, then come orangutans. The number of shared gestures in each subfamily appears in the tree as well.

**Fig. 1.10.2**




The distribution of gestures across living great ape species and genera, based on current knowledge: numbers of gestures specific to each species are shown, revealing extensive overlap. Notably, 36 gestures are shared among all apes, 30 additional ones are shared by African apes, and 3 additional ones are shared by bonobos and chimpanzees.

*Credits:* Figure redrawn by L. Ravaux.[32]

The reasoning we developed to reconstruct the history of *booms* can be applied again: very roughly, it is likely that approximately 36 gestures were already present in the most recent common ancestor of the great apes, which lived approximately 16 million years ago. And an additional 30 gestures are likely to have been present in the most recent common ancestor of African apes (chimpanzees, bonobos and gorillas), which lived about 8 millions ago. While the state of human language a few hundred thousand years ago is still a mystery, we have now gained extraordinary time depth concerning the evolution of ape gestures.

**Back to humans:** But there is an important character missing from our discussion: us! We are more closely related to chimpanzees and bonobos than they are to gorillas, as seen in the tree in Fig. 1.10.2. The most recent common ancestor of chimpanzees, bonobos and gorillas also had *us* as descendants. If this common ancestor transmitted something like the 66 gestures to its ape descendants (the 36 great ape gestures and the 30 additional African ape gestures), shouldn't we have inherited some of these gestures as well?

This is the current frontier. Initial results are tantalizing. Researchers from Hobaiter's team observed 13 1- and 2-year-old human babies interacting with each other – one group was in Germany, the other in Uganda. They described their communicative gestures with the same methods and criteria as they had used when observing chimpanzees in the wild. 50 of the infant gestures they described (96% of the total) seem to be part of the great ape lexicon, and among those, 46 (89% of the total) are shared with chimpanzees. The next step will be to determine what relation, if any, these infant gestures bear to our linguistic communication. As things stand, we just don't know: they might be an entirely different system, or they might have the seeds of human language. These are exciting times in ape and gesture research.

## *1.11 Conclusion*

Primate calls and gestures have meaning, in the sense that they convey information about the world. But does that make them language-like? After all, yawning, coughing and laughing convey information as well, but we wouldn't treat them as being linguistic in nature. In the end, it all depends on what one means by 'language'. But more substantively, in the following chapters we will come to precise conclusions about how meaning works in human language, and how different it is from what we found in primate calls and gestures. In particular, one thing is clear: human language is characterized by a sophisticated syntax that feeds into meaning – and thus *Robin loves Casey* doesn't mean the same thing as *Casey loves Robin*. There is currently no evidence for this sort of syntax in non-human primates. This doesn't mean that their communication system is uninteresting. First, there is at least one case, that of Campbell's *-oo*, in which a suffix can be added to a root (*krak* or *hok*) to form a new call with a different meaning. Second, there are arguments for an Informativity Principle in primates, one that is reminiscent of some principles of human communication (to be revisited in greater detail in Chapter 10).

Do we know what relation these systems bear to human communication? No, with one possible exception. Like some primate calls, ape gestures are remarkably well preserved over millions of years. This makes it possible to reconstruct the evolutionary history of ape communicative gestures in chimpanzees, bonobos and gorillas, among others. But this also suggests a tantalizing possibility: gestures that are shared among these three species would be expected to exist in humans as well. Initial work on infant gestures suggests that this might indeed be the case.

Finally, primate communication raised some of the main questions of meaning studies in general, those we will be concerned with in the rest of this book (they are summarized in the table below). What are the elementary pieces of meaning? We saw quite a few calls and gestures, and even a call suffix, *-oo*. How are these elementary pieces put together – what is their syntax? Things were a bit disappointing in this respect, although Campbell's *boom* arguably comes with a syntactic rule. What do the calls and gestures mean – what is their semantics? And are there further principles that constrain their use – what is their pragmatics? We saw at several junctures that there was much interesting action in the interplay between semantics and pragmatics. In particular, postulating an Informativity Principle proved illuminating to explain Titi and Campbell's calls. We even saw that chimpanzees appear to know another pragmatic principle (the Economy Principle), according to which one shouldn't state the obvious. Last, but not least, chimpanzees taught us to expand our view of communication so as to include the gestural modality. We will see all these questions arise in human communication – but in an incomparably richer form.

(The rest of this book is primarily concerned with meaning and thus with semantics and pragmatics, but an understanding of morphology and especially syntax will sometimes be important. In addition, rules pertaining to the elementary perceptual units of language – audible ones in spoken language, visible ones in sign language – are the realm phonology. If you wish to have a bird eye's view of phonology, morphology and syntax, you can refer to the brief appendix at the end of this book.)

| | **Definition** | **Non-human primate examples** | **English examples** |
|---|---|---|---|
| **Morphology** | = rules to construct (some) calls/words from smaller meaningful units | Campbell's monkeys<br>krak → krak-oo<br>hok → hok-oo | inform → informative<br>green → greenish<br>blue → bluish |
| **Syntax** | = rules to construct sequences/sentences from calls/words | Campbell's monkeys<br>*Boom boom* (usually) appears as a pair at the beginning of sequences. | *Robin loves Casey* and *Casey loves Robin* are well-formed.<br>*Loves Robin Casey* is ill-formed. |
| **Semantics** | = rules that determine the literal meaning of expressions | Titi monkeys<br>The A-call is true (appropriate) just in case there is a serious threat up. | *Robin loves Casey* is true just in case Robin loves Casey. |
| **Pragmatics** | = rules by which one reasons on the speaker's intentions to obtain further information | Informativity Principle<br>Use the most informative call available<br>(e.g. Campbell's monkeys, Titi monkeys). | Informativity Principle<br>Use the most informative word available. |

| | | | |
|---|---|---|---|
| | | Economy Principle<br>Do not state the obvious (e.g. chimpanzee use of the snake alarm call *hoo*). | *It is possible that Russia influenced the 2016 election* implicates that *it's not certain that Russia influenced the 2016 election*.<br><br>Economy Principle<br>Do not state the obvious.<br><br>*Look, there's a snake!* shouldn't be uttered if it's already obvious that there's a snake. |