

Part 1  
Empirical Investigations  
on Human Language

## 2

# Evolving Meaning: The Roles of Kin Selection, Allomothering and Paternal Care in Language Evolution

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### 2.1. Introduction: The Componential Approach to Language

Many contemporary scholars agree that future theories of language evolution need to take a componential approach to language that breaks human language into separate mechanistic components such as vocal imitation, syntactic abilities, and propositional semantics. In this chapter, I discuss the evolution of the last component – the abilities and proclivities underlying honest, complex, propositional meanings. This is both a critical component of language, and one whose evolution is the hardest to explain, precisely because of its apparent uniqueness. Nonetheless, I argue, the comparative approach has important insights to offer in this domain. I briefly discuss the hypothesis that kin selection played an important, but neglected, role in driving the evolution of rich semantic communication. I then review several bodies of comparative data not addressed in previous discussions. In particular, I discuss three related issues: 1) hominid life history, and our extremely long period of dependent childhood, 2) the flexible extractive foraging techniques typical of both modern humans and chimpanzees, and thus presumably present in our last common ancestor, and 3) the evolution of male parental care that typifies humans but not other great apes. I argue that these three factors combine to provide a unique selective regime that drove our ability and propensity to express semantically-complex concepts. I also discuss why sexual selection is unlikely to be adequate, by itself, to drive all elements of language evolution (and particularly semantics), but discuss the role that the evolution of male parental care might have played in “equalizing” the sexes, such that traits originally evolved in one or the other came, today, to be expressed equally in both.

The first step in devising adequate theories of language phylogeny and function is to recognize the complexity of language and acknowledge that no single cause,

factor, function or explanation can explain “Language” as a whole. Despite a persistent tendency of theorists to highlight one factor in the belief that the rest will just “follow naturally”, the search for single causes in language evolution has a long history of failure. An adequate explanation will require theorists to break down language into relevant components, highlighting and clarifying the specific mechanism(s) under discussion. Only after such fractionation can hypotheses about function or phylogeny be intelligently stated and tested, and only after progress has been made in this vein can we hope to combine the results in a model that encompasses the evolution language as a whole. There is no reason to believe that this eventual unification will ascribe the same causes or timing to each component of language, and many reasons to believe the contrary. Different components of language might have evolved at different times in hominid evolution, or under different selective regimes, reducing attempts to state precisely when “Language” evolved into mere terminological debates about what “the key” factor in language is. For these reasons, most theorists today accept the need for (at least) two stages in language evolution (Hauser, Chomsky & Fitch, 2002). Early hypothetical stage(s) before fully-modern human language can be termed protolanguage(s) (Arbib, 2005; Fitch, 2005b).

Acknowledging the methodological imperative to fractionate language is obviously simply a starting point for an adequate theory of language evolution. “Carving nature at the joints” to achieve a proper fractionation will be a non-trivial endeavour. Elsewhere I have argued for a basic fractionation into at least three components, each representing novelties required in human language evolution. This fractionation is either explicit or implied in most contemporary theories of language evolution (Fitch, 2005b). I have termed these components, for convenience, signal, syntax, and semantics. The most obvious requirement for externalizing language is a flexible, shared **signal** complex enough to convey novel thoughts. Because the dual desiderata of flexibility and conventionality (that the signals be shared by at least two communicators) entail an ability to learn signals (rather than having innate signals, as in honeybees or vervet monkeys), shared complex signals require a mechanism for vocal or manual imitation. In particular, the evolution of speech requires a mechanism for complex **vocal learning** which is not present in our nearest cousins, the chimpanzees, and indeed does not appear to be possessed by any nonhuman primate (Janik & Slater, 1997). Because the data against complex vocal learning in chimpanzees is very robust, complex vocal imitation is in some sense the most obvious mechanism that *must* have evolved at some point during hominid evolution. The fact that apes have richer gestural imitation abilities that may have paved the way to spoken language, does not explain this basic necessity away. I have shown elsewhere that peripheral anatomy of the vocal tract or larynx is not the crucial factor keeping chimpanzees or other mammals from vocal imitation (Fitch, 2000; Fitch, 2002; Fitch & Reby, 2001). The basic limitations that keep most mammals, and all nonhuman primates, from imitating complex vocalizations are therefore likely to be neural.

Fortunately, selective pressures potentially capable of driving the evolution of vocal learning are not hard to come by. Vocal learning has evolved multiple

times in parallel in at least six lineages (among mammals in humans, cetaceans, and seals, and among birds in hummingbirds, parrots, and songbirds). Simple vocal learning is also present in bats, and perhaps other clades. In the majority of these species, vocal learning supports complex songs produced by males only, and these are produced during the breeding season. Since Darwin, such songs have been believed to result from sexual selection (Darwin, 1871). Thus, from a comparative viewpoint sexual selection is a plausible default assumption for the evolution of complex vocal imitation as seen in animal “song” (Fitch, 2005c, 2006). However, it should be noted that there are other possibilities, and that we need to keep an open mind about the selective pressures that drove the evolution of human vocal imitation. In particular, sexually-selected mechanisms in mammals are typically expressed only (or preferentially) in males, and typically appear only at puberty (when they become useful). In humans, of course, vocal abilities are basically equal among the sexes, and if anything, biased towards females (Henton, 1992; Hyde & Linn, 1988). More striking and obvious is the fact that vocal imitation develops long before puberty in humans, with auditory learning starting before birth and imitation already well developed at age two, at least a decade before sexual maturity. Thus, although sexual selection might provide an initial drive towards vocal imitation, it seems unable to fully explain its current pattern in humans. This idea that other selective forces can drive or influence song is consistent with the repeated evolution of female song in birds, and its shared distribution and early maturation in some other clades such as dolphins. However, with these caveats in mind, the repeated evolution of complex vocal learning in vertebrates suggests that the evolution of this capacity is not the major puzzle in understanding language evolution.

The evolution of **syntax** is much more of a challenge, for a number of reasons. First, from a purely methodological viewpoint, syntax is less clearly defined than the speech signal, and far more difficult to operationalize for behavioural testing in animals. At the simplest level, simple sequential grammars, which restrict the order of different call or song components, have been known in animal communication systems for many years (Balaban, 1988; Hailman & Ficken, 1987; Robinson, 1984). For instance in the “chick-a-dee” call of the black-capped chickadee *Parus atricapillus*, “chick” notes always precede “dee” notes, and the latter can be repeated without any clear limit. This constraint can be written as a simple formal grammar (“formal” meaning that no changes in meaning are implied by changes in structure), at the finite state level (Hailman & Ficken, 1987). Similarly, analyses of chimpanzee “sentences” in the plastic block language used by Premack (Premack, 1971), the gestural system studied by Terrace (Terrace, 1979), or analyses of humpback whale song (Payne, 2000; Payne & McVay, 1971) reveal rule-governed restrictions on symbol order that can be considered a simple form of syntax, again at a purely formal level. More recently, the presence or absence of a “boom” note in forest monkey calls has been shown to influence the interpretation of the following vocal output, which represents an addition of semantic interpretation of a “syntactic” aspect of the signal (Zuberbühler, 2002). Thus, there are abundant aspects of signal structure

in animal communication systems that represent simple forms of grammar in either a purely formal sense, or in a few cases with added semantic implications.

Of course, human syntax goes far beyond simple restrictions on the order of elements. A core fact recognized by modern linguists is that human languages require grammatical systems that go beyond simple sequential ordering (grammars at the finite-state level) to include such factors as co-indexing and hierarchical embedding. A crucial part of the productivity of language, and its expressive power for representing thoughts, is that complex, hierarchically-structured *semantic* structures can be syntactically realized in the signaling system by various devices based on recursive embedding. For instance, any complex proposition  $x$  can be embedded in the sentence frame “I don’t believe that  $x$ ”, and this can be further embedded in other similar frames *ad infinitum* (e.g. “Mary thinks that I don’t believe that  $x$ ”). Such embedding is crucial to all human languages. Unfortunately, though, this intuition is quite difficult to apply to animal communication systems (Fitch, 2005a). How can we ask a humpback whale whether its apparent embedding has this property, if the whale’s song has no semantic meaning? One empirical approach is to back away from this difficult question to a more basic one: can animals recognize signals that are structured by rules powerful enough to capture such semantic embedding? Thus, Marc Hauser and I have developed an assay to probe for an animal subject’s ability to recognize strings in a simple context-free grammar (Fitch & Hauser, 2004), finding that cotton-top tamarins are unable to master a very simple grammar at this level, despite their ability to master a closely-matched grammar at the finite-state level in the same test situation. Humans find this context-free grammar trivially easy to recognize. Because human languages require grammatical power above the finite-state level, animals who are limited to this level would be unable to perform the syntactic computations necessary for human language. If another species (e.g. songbirds or great apes) can be shown to achieve the context-free level, we could further probe their abilities regarding the “mildly context-sensitive” level of grammatical power thought to be required for human language (Joshi, Vijay-Shanker & Weir, 1991). Thus, studies of this sort provide one way to investigate the grammatical abilities of animals at a purely formal level without requiring any semantic content in the signals.

The most difficult remaining issue is thus that of **semantics**, or the ability to express complex flexible meanings via signals. Although animal communication systems such as honeybee dance or vervet alarm calls clearly have semantic content, the flexibility of these systems is strictly limited. Indeed, the vervet system is based on signals whose structure is innately determined rather than learned, and even the semantic content of these signals appears to be largely biologically determined, with learning required only to narrow down the range of meanings. Furthermore, monkeys do not appear able to represent others’ minds, a key requirement of intentional, declarative semantics (Cheney & Seyfarth, 1990). A female monkey who watches food being hidden in a chamber does not make food calls when her young infant is subsequently released into it. More strikingly, when an infant is released into a cage where the mother has watched a predator hide, she does not increase her rate of alarm calling over baseline. Indeed,

although recent data indicate that chimpanzees are able to follow gaze and understand that “seeing is knowing”, this ability appears only in competitive situations and is never deployed in a cooperative, informative situation (Hare, Call, Agnetta & Tomasello, 2000; Hare, Call & Tomasello, 2001). Chimpanzee gestures are limited to imperative acts (e.g. reaching with outstretched hand to “beg” for food), and even basic declarative gestures (such as pointing, holding up objects for others to see, or even handing objects to others) are not observed in wild great apes (Tomasello & Call, 1997; Tomasello, Call, Nagell, Olguin & Carpenter, 1994). Together, such data on nonhuman primates suggests that the ability of humans to represent others as intentional mental beings, and particularly to be intentionally informative based on an understanding of what a conspecific does or does not know, may be unique to our species. This mechanism that underlies intentional, propositional semantics thus appears to represent another critical component to be explained in language evolution, and one of the most critical (Tomasello, 2003).

In this paper I will address the functional and phylogenetic basis of this latter component of meaning in language: the intentionally informative, highly complex semantics of human language. The critical starting point is the comparative data just discussed, suggesting that our nearest cousins lack the ability (or, at least, the propensity) to communicate in an intentional, informative, propositional manner. As stressed above, my discussion is concerned only with the evolution of this crucial semantic communication component of language, and *not* with the evolution of language as a whole. I am particularly interested in understanding the forces that could lead to **displaced symbolic reference** – the ability to talk about past events, or future plans or goals. I have argued elsewhere that communication among kin played a crucial role in the evolution of these key semantic aspects of language. I will recap this argument briefly below. However, it is plausible (and even likely, in my opinion) that other aspects of language evolved under different selective regimes, and at different times, as suggested above. In particular, the comparative data render it likely that vocal imitation may have been driven by sexual selection, and may have preceded the evolution of meaningful language, as in Darwin’s “musical protolanguage” hypothesis (Fitch, 2005c; Mithen, 2005). But if this is true, it raises the question of how an initially sexually-selected trait (a type that is almost invariably sexually dimorphic) became evenly distributed among the sexes, and came to develop long before maturity, in modern humans. The inverse question applies to the sharing of information among adults and young, which might be expected to be mainly expressed by females. I will argue that a role of males in parenting, an unusual facet of human biology, helps to explain this transformation and equalization.

## 2.2. Kin Communication and the Evolution of Meaning

I have previously suggested (Fitch, 2004) that kin selection provides a plausible but neglected selective regime relevant to a particular component of language: its capacity to convey complex propositional meaning. As already suggested above,

attempts to explain this factor based only on sexual selection are unconvincing because of the early development and lack of sexual dimorphism in our abilities to communicate semantically.

The kin communication hypothesis is simple and relatively intuitive, making its neglect in previous discussions of language evolution somewhat puzzling. The hypothesis suggests that the selective force behind honest, semantic communication was the sharing of information among kin, and particularly between adults and their offspring or young relatives. This hypothesis solves a critical problem in the evolution of communication that has been extensively discussed outside the context of language evolution: the evolution of “honest” communication systems (Maynard Smith & Harper, 2003). What are the selective forces that favour the evolution of signals that convey useful information between individuals? This turns out to be a significant theoretical problem, because in many cases communication is appropriately seen as an “arms race” between signalers and receivers, where there are few or no incentives to emit honest signals, but many to exaggerate or bluff. Rather than a world of animals openly sharing information with one another, the modern picture is one of animals who selfishly emit signals when it benefits them to do so. In many cases of communication between adults (e.g., signals concerning courtship or territoriality) it will often benefit to mislead or exaggerate (Dawkins & Krebs, 1978). This in turn benefits receivers who are skeptical “mind readers”, rather than gullibly accepting signals as valid (Krebs & Dawkins, 1984). The mechanisms by which “honesty” can be ensured (or at least partially encouraged) are rather limited (Fitch, 2002; Maynard Smith & Harper, 2003): signals may be automatically honest because of the signal production mechanism or similar constraints, or honesty can be guaranteed by handicaps. The handicap principle (Zahavi, 1975, 1977) suggests that *only* costly signals can be stable over evolutionary time, and more recent theoretical treatments further entail that handicap costs must vary with signaler quality (Grafen, 1990). Despite the intense theoretical and empirical interest in handicaps in recent years, it has long been clear that handicaps cannot account for honesty in human spoken language, because speech is an extremely low-cost signal (Zahavi, 1993). While certain information may be conveyed honestly by default in speech, physical constraints are clearly inadequate to drive semantics (Fitch, 2002). So what options are left?

The alternative to “guaranteeing” honesty in a Machiavellian world with some aspect of the signal itself is provided by situations in which it is in both communicators’ best interest to communicate honestly (“best interest” in terms of increasing their long-term inclusive fitness). Specifically, if it is in the signaller’s interest to share information honestly, and the receiver’s to accept this information unskeptically, honest communication systems can evolve without any signal-internal guarantees necessary. Such conditions are provided neatly by kin selection if communication is preferentially directed towards kin (that is, honest signals are preferentially emitted in the presence of kin rather than others). In such a situation, the system need only satisfy Hamilton’s inequality  $C < Br$  (the *Cost* of signaling to the signaller is less than the *Benefit* obtained by the recipient,

diluted by the fraction of relatedness  $r$ , a number between zero and one) to be evolutionarily favored. Given that vocal signals, and speech in particular, are low cost signals, this is not a particularly stringent requirement. Thus, kin selection on kin communication systems can easily drive the evolution of meaningful signals, neatly avoiding the dual traps of Machiavellian deceit and Zahavian handicaps. Once a communication capable of honestly conveying complex concepts has evolved via kin selection, it can then be utilized among non-related individuals via reciprocal altruism (Trivers, 1971), allowing the type of carefully-metted-out information among unrelated adults that we see in humans today. See (Fitch, 2004) for a more detailed and rigorous exploration of these ideas.

In the remainder of this paper I will outline some new arguments based on hominoid life history, ape foraging tactics, as well as human mating and childcare practices that I see as providing additional support for this “kin communication” or “mother tongue” hypothesis. The first issue addresses the question of why kin selection has not led to language in many more species. The second issue, not unrelated, is what specific aspects of human social behaviour could have licensed the transition from a hypothetical sexually selected “songlike” communication, expressed preferentially in males, to the sexually-egalitarian distribution of language abilities (and musical abilities, incidentally) that we see in modern humans. An understanding of both of these questions, I suggest, requires us to delve deeper into some well-known aspects of human biology that have rarely been integrated into discussions of language evolution.

First, given that kin selection is a ubiquitous force among group living animals, one might be justifiably skeptical about its *specific* significance in human communication. Put bluntly, if kin communication is enough to drive honest meaning, why haven’t honeybees, songbirds, ground squirrels and many other species evolved language? There are two parts to the answer. First, most obviously, communication of complex thoughts requires a shared signaling system of comparable complexity. The lack of signal learning in most species means that, for most animals, such a system is unavailable (as discussed earlier). Only in species in which the mechanisms underlying complex signal learning are present already, in at least rudimentary form, can kin selection begin to drive complex symbolic communication. As already discussed, there are various phylogenetic routes to the evolution of learned signaling systems, but one of these must have already been taken to allow entry into this selective regime. From this viewpoint, the question becomes more limited to those species that have a system of vocal learning. Why don’t songbirds, parrots, seals or cetaceans use their complex vocally-learned signals to transmit complex thoughts as humans do?

This brings us to the second part of the answer, the component more relevant in the context of this paper. The value of a complex communication system depends on the existence of complex thoughts which are worth conveying. That is, there must be some way in which successfully conveying thoughts would actually increase inclusive fitness. If cognitive representations are quite limited, this will provide an intrinsic limit on the concepts communicated, and thus on the value of communication. This is clearly relevant to species like honeybees, which



are short-lived and have little relevant information to share with their sisters other than the location of food, water and nest sites. It is less obvious that this limit applies to birds, some of which have complex cognition rivaling that of nonhuman primates (Emery & Clayton, 2004) and thus might in principle have plenty to talk about. However, the period of parental care in songbirds is generally very short, so there is a time limit typically of a few months, and generally of less than a year, in which valuable knowledge acquired over a parents' lifetime might be imparted to its children (the upper end would be species with "helpers at the nest" with a contact time of less than two years). This is also the case for pinnipeds such as phocid seals, which generally have very short periods of maternal care (including the shortest of all mammals in the hooded seal *Cystophora cristata*). Finally, for marine mammals such as dolphins or killer whales, which are both intelligent and can have long term associations with their young, it is not clear that a mother's knowledge, if transferred to her young, could greatly increase her offspring's survivorship. The limited foraging demands involved in catching fish may not provide an adequate selective basis for a rich system to convey learned knowledge (alternatively it remains possible that some cetaceans do have undiscovered abilities in this direction).

In the next section I will argue, based on comparative data from other great apes, that the situation in our prehuman ancestors differed significantly from that of these other animals. The starting point will be the evolution of hominids *sensu strictu* starting with our divergence from chimpanzees about 7–8 million years ago. This was the time of our **last common ancestor** with chimpanzees, the LCA. The LCA was an African ape, probably confined to the forests stretching across the middle of Africa. We have essentially no fossil record for this species, although new fossils from this time period give considerable hope for future discoveries (Brunet et al., 2005). In order to reconstruct the lifeways of the LCA we thus need to turn to the comparative method, focussing particularly on the great apes. In the interest of brevity I will use the colloquial term "chimp" below to refer to both chimpanzees and bonobos, and will use their full names only when it is necessary to distinguish them. The discussion is based on data reviewed in (Aiello & Key, 2002; Boesch & Boesch-Achermann, 2000; Diamond, 1992; Goodall, 1986).

### 2.3. The Ape's Impasse: The Hominoid Mother's Dilemma

Primates are rather unusual mammals from a reproductive viewpoint. In sharp contrast to the large litters of puppies, kittens, piglets, or mice borne to most mammalian mothers, most primate mothers have just one child at a time (though twins are normal in a few species). Furthermore, this one child has an unusually long period of dependence on its mother: in most monkeys the infant is completely dependent for a year, and then still associates with its mother in a protective, affiliative relationship for years after that. But even by primate

standards, apes are extreme (I use the term “hominoid” to refer to humans + apes, reserving the traditional term “hominid” to refer only to humans and their post-LCA ancestors). A chimpanzee infant is completely dependent on its mother for transportation and milk for at least two years, and more typically four, and the typical inter-birth interval for chimpanzees is between 5 and 6 years (Boesch & Boesch-Achermann, 2000). In the same period of time, a rhesus macaque female can already have grandchildren. The combination of low reproductive rates, long interbirth intervals and a lengthy childhood (including a longer period to sexual maturity – 10 years to sexual maturity for a female chimp) puts apes at a reproductive disadvantage relative to virtually all mammals their size (only elephants or whales have similarly long reproductive times: interbirth intervals of 3–4 years for African elephants and 2–3 years for humpback whales). With these powerful forces restricting her total lifetime reproduction, a female ape can meet her reproductive potential in only one way: survival – both of herself and of her offspring. Thus it is not surprising that apes (like whales and elephants) are also very long-lived, and very solicitous parents. Only by living a long time, and making sure that each of her precious children in turn live a long time, can the reproductive equation be balanced. Increasing any of the factors on one side (interbirth interval, gestation time, infant dependent period, or time till sexual maturity) decreases reproductive potential, and only a compensatory increase in the mother’s own longevity can counteract them. In particular, the long period of childhood dependence means a long interbirth interval, and there seems to be no way around this impasse. This dilemma applies to all apes, including humans.

One of the many ways in which the *scala natura* caricature of evolution has clouded our vision is in the relationship between apes and monkeys. Because monkeys (which in the current context means Old World monkeys, cercopithecids) are supposedly lower on the great chain of being, there is a tendency to assume that they were dominant earlier in evolution. But the available paleontological evidence suggests that this prejudice gets the facts almost backwards. About 15 MYA, dryopithecine apes (ancestors of living great apes and humans) were widespread throughout Africa and Asia, while monkeys were quite rare. But the situation changed abruptly around the Miocene/Pliocene border, perhaps due to the climate changes and breakup of the once ubiquitous gallery forests into a mosaic of forest and grassland. The fossil record does not typically allow us to reconstruct what happened in detail, but in cases where it is adequate (e.g. Pleistocene East Asia), monkeys succeeded during periods of ecological instability, while apes disappeared, or were relegated to patches of stable rainforest (Jablonski, 1998). Today, the result of this difference is clear: monkeys dominate, and modern apes are confined to pockets of isolated forest. Monkeys, with their high reproductive rates, have taken over in most of the areas where apes once dominated. Indeed, apes today can be thought of as relict populations of a once-dominant clade, the last hangers-on in the most stable and welcoming environments. The monkeys’ victory cannot be due to greater intelligence, more efficient food use, or direct physical competition – in all of these respects apes clearly outclass monkeys. Apes (sometimes literally) “eat monkeys for lunch”.

So why are monkeys so successful today, and how did they displace the once-dominant apes? The only clear advantage is their much higher reproductive potential, particularly in situations of climatic change where high intelligence and large body size can no longer necessarily assure a long life.

There is, of course, one group of apes that somehow evaded the ape's impasse: the line leading to humans. But although we might, out of habit, think that it was our use of tools and our high intelligence that allowed us this demographic victory, the fossil record makes us think again: our first assured hominid fossils have brains no larger than a chimp, and no remains of material culture more sophisticated than those of a chimp (Cameron, 2004). But they had already moved into the drier, more variable mosaic environment that no other apes were able to occupy successfully. They were already bipedal, but it is not clear why this should have proved demographically advantageous. But if we examine modern humans today, we have another advantage over our ape cousins: our unusual system of shared child care gives modern humans a much higher reproductive potential than either a chimp, gorilla or orangutan. A human mother outreproduces any chimpanzee female through the simple expedient of having babies faster (Lovejoy, 1981). According to simple demographics, by having babies every 2–3 years instead of every 5–6 years, we humans (and this includes hunter gatherer mothers, not just supermarket-fed Western mothers) have found a way out of the ape's impasse. And the rest, we might say, is history. But if this solution is so easy, why haven't other apes done the same thing? Why don't chimp mothers simply wean earlier? The answer has become quite clear with recent studies of chimpanzee demographics (Boesch & Boesch-Achermann, 2000). Earlier weaning means poor survival of the young, and ends up leaving them smaller and less able to compete with other chimps whose mothers have fed them up to their full potential body weight.

It is revealing to look at the situation from a chimpanzee mother's perspective (Pusey, Williams & Goodall, 1997). Your infant will ride on your back and nurse, deriving all of its protection and nutriment from you for its first year, much like a human infant. However, your infant will continue to nurse consistently till age two, when solid food becomes an appreciable component of its diet, and will continue nursing periodically until between four and six years old. At age four, although it can locomote by itself, the child will still need to ride on your back for long voyages, and it is still mainly dependent on food you share with it. Weaning at this point could be disastrous – if conditions change suddenly and no food is available for your child, it still lacks the reserves and intelligence to survive on its own. From the child's viewpoint, none of this is very different from the human situation. The big difference is that, because she has weaned her child from breast milk much earlier, the human mother has already given birth to another child, and is raising two (or more) children in parallel. In a situation of superabundant, reliable food (e.g. the situation a grazing animal in a huge grassland faces with its offspring) this is clearly an excellent solution. Unfortunately, this is not the situation that faces chimps, or that faced our hominid forebears: although fruiting trees may

present pockets of superabundance, they can be interspersed with long periods of want. At such times, difficult learned skills such as nutcracking, termite fishing, or exploitation of unpredictable food resources encountered only rarely, may provide the main source of rich nutrition (Boesch & Boesch-Achermann, 2000), and mean the difference between starvation and survival. There is no easy way that a chimp mother could double her child's food intake until that child is also competent at such complex foraging skills. The value of potentially sharing knowledge with offspring is, so to speak, "built in" to the chimp/human lineage by our reproductive biology and the resultant demographics, as well as the fact that we are generalist foragers dependent upon complex, learned extractive foraging techniques for survival. With the increased importance of cooperative foraging techniques (including scavenging, hunting, fishing and complex food processing) in our own lineage, these advantages would be even greater, giving a positive feedback loop between semantic communication and complex foraging.

Summarizing, an unusual combination of very slow reproduction, and uniquely extended childcare, with reliance on complex, learned foraging, characterized the LCA of the chimp/human lineage *before* we evolved language. I suggest that this situation (which is not speculation, but is based upon the actual observed behaviour and demographics of living apes and humans) provided an important precondition for the evolution of symbolic reference and intentional semantic communication in the hominid lineage. With some appropriate learned signalling system in place, such a situation would provide an excellent driving force for the honest, low-cost communication of complex concepts that we seek to explain. As already suggested above, there are several (independent) ways to evolve a complex learned signaling system, including sexual selection (Darwin's "singing ape" hypothesis) or various other possibilities (see Fitch, 2006). Combined with such a signaling system, we can perceive a definite, quite unusual, Darwinian advantage that our ancestors would have derived from the intentional sharing of ideas with other individuals. Although I have focused on mother/infant communication, it is clear that sharing of information among other kin (e.g. by grandmothers or siblings) would also increase the communicators' inclusive fitness. Thus a critical factor in explaining why kin selection drove the evolution of language in humans (but not other mammals known to have complex, shared signaling systems) is the long period of dependence combined with a crucial reliance on regionally-variable, complex, learned extractive foraging techniques: factors that characterize both chimpanzees and humans.

But what about fathers? The situation described so far inverts the difficulty already discussed that faces hypotheses based on sexual selection: predicting male-specific traits. By this model, we might expect human females to produce linguistic utterances and males to simply comprehend them (allowing male offspring to understand their mothers). At best we might expect intentionally informative male speech to be directed at siblings at an early age, but adult males should mainly produce meaningless songlike utterances. So there is still potentially a gap to be bridged between the predictions based on kin

communication, and empirical reality. Why do adult males have meaningful language? Can the comparative database, or even fossils, help to clarify this apparent contradiction?

## 2.4. Male Parental Care in Humans and Other Vertebrates

Returning to the ape mother's dilemma, enter the male of the species. From the viewpoint of a female ape, adult males are basically a waste of resources, useful as sperm donors and little else. Males eat a lot, are often behaviourally dominant and can displace her or her child from food, but provide little or nothing in terms of childcare. Male primates and males of many other mammal groups may even kill the current crop of offspring to speed mothers' readiness to mate and produce new offspring. While male chimps preferentially hunt for meat, they mainly eat it themselves, partitioning it among the other (mostly male) hunters. Because a mother carrying a dependent child is not much use in the acrobatics required to catch a monkey during chimpanzee hunting, all she can hope for is a few scraps of meat for herself, obtained by tolerated theft from the hunter, and little or no meat for her child (Boesch & Boesch-Achermann, 2000). Thus, although potentially a rich source of additional nutrition, the meat caught by male chimpanzees contributes little or nothing to a mother's needs. The best we can say for male chimpanzees is that they provide a degree of protection, both from predators like leopards that can be a significant source of mortality for young chimps, and from the potentially infanticidal males of neighboring groups. These defensive advantages accrue to all members of the group. But from the viewpoint of feeding any particular baby, a mother chimp can forget about the males – unless there were some way to entice a male to contribute more specifically to her particular child. Thus, one crucial factor in human evolution that helped to solve the hominid mother's dilemma was the evolution of male parental care.

The importance of male paternal care in modern humans has long been known, and there are numerous empirical data supporting a critical role for an involved father in increasing infant survival in many cultures. Given the lack of such evidence in our nearest cousins (chimpanzees and bonobos), this appears to be a critical biological change in our species. Unfortunately, the fact that human males have an unusual potential for parental care has been over-extrapolated into a wide range of more dubious precepts about human behaviour, often including moral undertones, and the resulting complex has been repeatedly (and rightly) challenged in recent years. A caricature of a particularly long-standing model ties together two suspect ideas, of "man the hunter" and the nuclear family, and runs along the lines that, first men started hunting, providing a potential bonanza of protein and fat for building bigger, healthier babies, and second, women traded sex for meat to craft the monogamous nuclear family that we know today. Despite several grains of truth to this picture, it is clearly overly simplistic, and contradicted in numerous ways by the facts. In order to extract the grains of truth and leave behind the dross, we need to clearly distinguish several distinct

issues and focus on the empirical basis and logical consistency for each of them. In particular we need to distinguish male paternal care (a social relationship between males and young who are often, but not necessarily, his offspring), pair-bonding (often termed behavioural monogamy – a social relationship between adult males and females) and sexual monogamy (indexed imperfectly by mating behaviour, but which ultimately boils down to the genetic facts about paternity: which adult males are the fathers of which young). Although these traits are often linked together in various ways, none of these links are inevitable. This means that the “prototypical” nuclear family, where there is a pair-bond and sexual monogamy between the parents, and the male devotes all of his paternal behaviour towards his mate’s offspring, is simply one extreme of a continuum, a restricted region of a more complex space of possibilities.

The “nuclear family” model has been empirically challenged from several directions. Perhaps the most scandalous to modern sensibilities is the high number of children in Western “monogamous” societies who turn out genetically to be the progeny of extra-marital affairs. But similar levels of “extra pair copulations” are seen in many behaviourally monogamous species with solicitous paternal care (e.g. many birds), so for a biologist this comes as no surprise (Dewsbury, 1988). Another challenge comes from anthropology, where the range of socially-condoned human mating systems is wide, and often highly variable even within cultures. For example, the majority of the world’s traditional cultures condone polygyny (though typically within strict limits that demand paternal care for all offspring). This fact squarely challenges the notion of social monogamy as “normal” human behaviour, but indeed emphasizes the cultural importance placed on male parental care in humans. The role of the father in childcare also varies considerably between cultures, and the benefits fathers provide to infants are not necessarily even measurable empirically in some cultures (Strassmann, 2003) (though in others, e.g. the Ache, they are large and undeniable (Hill & Hurtado, 1996)). Finally, increasing attention has been called in recent years to the role of alloparents – grandparents, siblings, uncles and aunts – in human childrearing. The most well-known version of this hypothesis, the “grandmother hypothesis” (Hawkes, O’Connell, Jones, Alvarez & Charnovs, 1998), suggests that post-menopausal grandmothers played a crucial alloparenting role in human evolution. Although sometimes seen as an alternative to hypotheses based on paternal care, most of the biological arguments put forth in support of the grandmother hypothesis actually carry through to all forms of allomothering, including paternal care, and these ideas are not mutually exclusive (Hrdy et al., 2004). Given that *females* other than the mother provide “aunting” of various sorts in a wide variety of primates, the thread that runs through all of this, and that remains to be explained, is the increasing role of *male* parental care since our split with other apes.

Do humans, as a species, exhibit male parental care? The answer to this question is certainly yes. The degree to which human males help care for children is quite striking to anyone who has spent time watching adult males of most other primate species. Not only are human males expected to help care for children in

all cultures, but in many polygynous cultures the male's ability to care for his multiple wives and their children is a prerequisite for legal polygyny. Even in cultures where the mating system leads to low paternity certainty, men help care for their sister's offspring. This of course does not mean that *all* fathers care for *all* of their children: human males seem to pursue mixed strategies in this regard. As discussed below, there is a good correlation between a monogamous mating system and paternal care among birds and mammals, so the existence of male paternal care in humans certainly suggests a degree of monogamy in our species. Furthermore, most males who have fathered extra-marital offspring nonetheless act as industrious fathers to their own (well, mostly their own) offspring. Thus, imperfect sexual monogamy is no barrier to the evolution of male parental care, and new genetic data on monogamous mating systems in nonhuman animals reveal them to be strikingly similar, in many cases, to the mating systems of humans (Dewsbury, 1988).

The changes in mechanisms underlying male social behaviour that underwrite paternal behaviour in our species are still poorly understood, but recent advances in understanding the genetic, neural, and behavioural bases of paternal care and pair bonding in other mammals suggests the possibility of major breakthroughs in the near future (Insel, 1997). Monogamous male prairie voles show a much more female-like expression of neuropeptide receptors (particular vasopressin 1a receptors) in their brains than closely related, but polygynous, meadow voles. Within the same species, males' variation in receptor densities is correlated with paternal care, and experimental upregulation of gene expression leads to enhanced attention to their offspring (Hammock, Lim, Nair & Young, 2005; Lim et al., 2004). These results suggest that rather subtle shifts in gene regulation can have important effects on these types of behaviours, and it should soon be clear whether similar genetic mechanisms are involved in humans. In any case, from a phylogenetic perspective, the realization that shifts in social behaviour can drive changes in the male brain towards a loss of sexual dimorphism suggests one possible route to derive a sexually-egalitarian distribution of traits that were once sexually dimorphic. A cognitive mechanism that originally evolved in a context of sexual selection, and was strongly sexually dimorphic, can end up being expressed in both sexes equally under a new selection regime favouring male parental care. This provides one way in which traits such as vocal imitation (posited by Darwin and many others to originally be preferentially expressed in males), or information sharing with offspring (predicted by the kin selection model to be preferentially expressed in females) could end up being more or less equally expressed in both sexes.

Returning again to the female ape's reproductive dilemma, our own hominid line found a way around the demographic impasse, a solution that was novel for apes but common among vertebrates: increased reliance on allomaternal, including male paternal, care (Hrdy et al., 2004). Although some authors have therefore seen a monogamous prototype of the paternal "nuclear family" at the beginning of hominid evolution (e.g. Lovejoy, 1981), there is no reason that male parental care necessarily entailed strict monogamous pairing. Once

interbirth interval decreases, it is in everyone's benefit to help the weanling survive (including not only the presumptive father, but also relatives like the mother's mother, or her brother (O'Connell, Hawkes & Blurton Jones, 1999)). A simple shift in a chimpanzee male's propensity to share meat with their previous consortship partners, and their own presumptive children, would be enough to start the ball rolling to the increased reproductive potential seen in modern humans. Again, these considerations reflect behavioural patterns observed in modern chimpanzees today, not imagined fairytales. Furthermore, such a shift to paternal care and restricted mating in the direction of sexual monogamy has evolved repeatedly among mammals, including most prominently the closest cousins to the great apes, the gibbons and siamang, all of which are behaviourally monogamous with some male parental care (probably with the occasional smattering of adultery). The same pattern has also evolved in the callitrichids (marmosets and tamarins) in which the solicitous support of fathers has made it possible for females to habitually give birth to twins, thus doubling at one stroke the reproductive output of a normal primate. Finally, behavioural monogamy, with paternal care, has evolved convergently in owl monkeys, *Aotus*. It is not surprising that monogamy has independently evolved multiple times among primates since primates are unusual among mammals in having such low reproductive potential in the first place. The trick for females is to somehow entice males to share parental care; the hurdle for males is high paternity certainty, and a tip in the balance of the trade-off between investing in current children vs. seeking additional matings from other fertile females.

## 2.5. Behavioural Monogamy and Paternity Certainty

In the free-for-all mating system that characterizes chimpanzees and bonobos, paternity is very uncertain, and male chimps typically have no way to know which child is their own. Furthermore, because female chimps emigrate out of the group, a male can't care for his sister's offspring either (unlike some human cultures, with high paternity uncertainty, where a sister's offspring are the target of male care). In highly polygynous apes like gorillas, the structure of the mating system itself guarantees that there will be other bachelor males in the vicinity, offering continual threat of "illicit" copulation and competition to the harem-holding males. In either case, the only way to reliably induce males to care for their children is to offer some degree of paternity certainty, and this requires a novel mating system: behavioural monogamy, often dependent on pair bonding.

Although uncommon in mammals, behavioural monogamy has evolved in parallel in many mammal clades, including various primates, most canids, and some rodents (Kleiman, 1977; Reichard & Boesch, 2003; Wickler & Seibt, 1981) as well as in some invertebrates (Wickler & Seibt, 1981). It is the main mating system in birds, with over 90% of bird species showing monogamy. In many species, there is a good overlap between monogamy and paternal care



(Clutton-Brock, 1991; Kleiman, 1977), though other factors certainly play a role (Reichard & Boesch, 2003). This, of course, makes perfect sense from an evolutionary viewpoint: a monogamous mating system (where a male and female pair off and stay together for the entire mating period) offers high paternity certainty. There is a point at which the evolutionary balance tips, and it becomes more beneficial for a male to help care for his own children and to help ensure their survival, than to abandon the mother after she is pregnant to seek another potential mate. This situation will often apply particularly in species with a short synchronized breeding system, where all females are fertile simultaneously (one reason that monogamy is so common in birds), in solitary species where mates are hard to find, or in areas where each female has a large home range and a male cannot defend multiple females effectively (Brotherton & Komers, 2003). None of these appear to be the case for humans, or for other apes: the spatial factors do not seem to apply, and we do not have the population-wide breeding season that many birds have. In contrast, female primates generally announce their own *private* breeding season – the oestrous period – to all comers. This can create intense competition for breeding among males, which in chimpanzees and bonobo typically results in multiple males (and often the entire group) mating with a fertile female, with concomitantly low paternity certainty. However, there is another strategy, even in chimpanzees, called “consortship”, where a male and a female disappear alone into the woods together during her oestrus period (Goodall, 1986). A similar potential strategy was probably present in the LCA, already offering a path to monogamy for the hominid line. By being more willing to enter into such consortships, thereby granting paternity certainty to her mate, a female ape could tilt the balance towards male parental care.

Are humans behaviourally monogamous? One does not need to be particularly perceptive about our species to realize that, in any strict sense, the answer is “no”. Despite the cultural imposition of legal monogamy in most widespread modern cultures, adultery is common (even in the face of extreme punishment). In most of the world’s traditional cultures, polygyny is accepted: a man may have more than one wife. Thus, the notion that humans are biologically monogamous seems almost laughably naïve or Eurocentric, given the frequent exceptions to monogamy in both Western and other cultures. However, from a comparative perspective, it is now clear that many monogamous species have similar deviations from strict or pure *genetic monogamy* (where all offspring produced are from the pair) despite clear behavioural or *social monogamy* (where males and females pair off socially beyond the mating period) (Reichard & Boesch, 2003). “Monogamy” turns out to be a rather diverse phenomenon, with a wide range of combinations of social, mating and genetic monogamy possible. In many “monogamous” species, DNA paternity tests have revealed a heretofore unexpected amount of hanky-panky – demurely termed “extra-pair copulation” by biologists. Furthermore, many other species practice serial or sequential monogamy, with pairs mating and raising children, but then choosing new mates in future reproductive seasons. Thus, our mistake was to think monogamy is an all-or-nothing package, and biologists now realize that a fairly high amount of adultery is compatible with a

behaviourally monogamous social system. By the definitions currently used by biologists, many human cultures, and most human sexual relationships, are typically socially monogamous, but genetic monogamy is less pervasive. But even social monogamy is quite rare in mammals (around 5% of all species), and demands an explanation (Clutton-Brock, 1991). Given the selective forces already discussed, what were the *mechanisms* that led humans away from the free-for-all system of chimps to the pair-bonding and partial monogamy seen in modern humans?

The factors that drove this change in our reproductive strategy have been discussed extensively and include most prominently the **concealed ovulation** of human females. There are many hypotheses for the precise function of concealed ovulation (for a light-hearted overview see (Diamond, 1992)), but one effect is clear - it tips the balance towards monogamy. Most primates copulate only while the female is in oestrous, and therefore fertile. A male who can either outcompete other males, or lure the female into solitary consortship, need only do so during this brief and obvious oestrus period in order to ensure his paternity. But human females do not advertise their fertility (even to themselves), but rather physiologically conceal it quite effectively, and therefore a much more extended period of exclusive copulation is necessary for males to achieve any paternity certainty. In the limit, well-concealed fertility “establishes mathematical parity between males restricted to a single mate and those practicing complete promiscuity” (p. 346 Lovejoy, 1981). It is important to note that most apes are more like humans than chimps: bonobos and chimpanzees are unique among apes in their redolent oestrous swellings and highly promiscuous mating patterns. It is thus likely the LCA was more like humans, orangutans or gorillas, with a relatively understated oestrus with little swelling or other obvious competition-inciting cues to her fertility. Physiologically speaking, humans have gone in one direction from this starting point, to unusually “invisible” fertility, while chimps have gone in the other. The critical point is that, with concealed fertility, male *mating* success (the number of females mated with) is somewhat decoupled from *reproductive* success (the number of offspring generated that survive). Put concretely, even a human male who mates with a different woman every night for one month is not *guaranteed* higher reproductive success than a male who mates with one woman every night over the same period. Unless they have some way of knowing when their mates are fertile, the two men may each conceive a single child from this pattern of mating. Of course, a woman is typically fertile for more than one day, so if the hyper-promiscuous male could keep up this performance, he would eventually out-reproduce the monogamous male on average. But, again, reproductive success involves not simply conceiving offspring, but raising them to maturity, and the human system of male paternal care may give an important advantage to the second male if he stays to help raise the child that he now *knows* he has fathered. Alternatively, the male may simply be coerced into this behaviour by the effective “trick” of concealed ovulation, along with social sanctions from females and their kin (as argued for callitrichids (Dunbar, 1995). Either way, the final outcome – male parental care in our species – is what matters.

In conclusion, at some point in its evolution the human lineage diverged from the other apes in its reproductive behaviour by extending the duties of childcare beyond the mother, in a manner familiar among other vertebrates. Although numerous perceptive scholars have recognized these facts (Deacon, 1997; Diamond, 1992; Hawkes, 1998; Hrdy et al., 2004; Lovejoy, 1981; Mithen, 2005), it is still insufficiently appreciated, particularly among students of language evolution, just how momentous a change this represented. The observations made in this section are based upon solid behavioural and paleontological data. Apes do face a reproductive dilemma, apes other than humans were mostly replaced by monkeys, and humans did evolve increased male parental care at some point. The critical remaining question is whether these facts are causally related. There is obviously no fossil evidence of direct male parental care (although Lovejoy has suggested that bipedalism itself is an adaptation to food carrying, and thus some indicator of food provisioning (Lovejoy, 1981)). Thus the evolutionary timing of this behavioural change in our species remains open. There are only two clear indicators present in the fossil record that are compatible with an increase in monogamy, both of which rely on the observation that monogamous species typically show a reduction in sexual dimorphism relative to their polygynous relatives. The first is the reduction in canine size overall, and a near-loss of canine dimorphism between males and females. This change was already in place in australopithecines (Johanson & White, 1979), compatible with the hypothesis that some reproductive changes occurred early in hominid evolution, well before expanded brains and increased tool use. The second indicator is the much later reduction in body size sexual dimorphism, thought by many authors to have occurred rather abruptly with *Homo erectus* (Kappelman, 1996). At this point, clearly, humans had shifted to something like our current system. Although I personally find the arguments of Lovejoy and others convincing – that the reproductive changes occurred very early – from the viewpoint of language evolution it makes little difference when these permissive factors evolved, since few commentators suspect the small-brained australopithecines of having language. By the time human language evolution was presumably underway (with the genus *Homo*), humans were less dimorphic than other apes, and the comparative data strongly suggest that this reflects an increase in male paternal care, and the (admittedly imperfect) behavioural monogamy that goes with it.

## 2.6. Conclusions and Prospects

To recap the argument presented here, a key issue preceding the evolution of symbolic, semantic communication in humans was the demographic dilemma faced by all great ape species. Our whole clade is characterized by very slow reproduction and very extended childcare, and this led to our clade's nearly complete replacement by faster-reproducing monkeys in the Pliocene. By shortening our interbirth interval, humans (alone among apes) have evaded the dilemma. One

component of this solution has been allomothering: mothers enlist other individuals to help with childcare, including their own kin (grandmothers and siblings) and more surprisingly (among mammals) the father of the child. The latter addition was achieved by far-reaching changes in male and female human biology, along with changes in the human mating system that function to provide increased paternity certainty, and a consequent evolutionary incentive for some human fathers to aid in the care of their children. A second core factor in my argument is the fact that both chimps and humans are generalists with complex, learned extractive foraging techniques that need to be mastered by youngsters before they can feed themselves, and long-term knowledge about the dangers and affordances of their environment – precisely the sorts of knowledge that language is useful to share. These factors constitute observable facts about apes and humans, and provide part of the known biological fabric for any theory of any aspect of human evolution. I have tried to show that they have particular relevance to an aspect of language that is both highly unusual (indeed, unique at the level of complexity seen in modern humans), and perhaps the most idiosyncratic characteristic of language as a whole: our use of vocal signals to convey elaborate propositional meanings. Together, these aspects of ape and human biology help to explain why some other species that have complex vocal learning have not evolved symbolic semantic communication. Birds do not face the hominoid reproductive dilemma; seals or cetaceans have neither the extended post-weaning childcare *nor* the necessity to learn complex extractive foraging techniques and exploit unpredictable food resources. These arguments also help to understand why species that have simple semantic communication systems, like honeybees, have not gone further on the road towards language: they don't have enough novel, complex concepts worth talking about to drive the evolution of a more complex and flexible system. Such a system would therefore provide no evolutionary advantage over a simpler, unlearned system like the dance language.

In the argument I have made here, the rarity of flexible semantic communication systems in the animal kingdom derives simply from the rarity of this combination of factors. No one of these factors is in itself unique; from a comparative viewpoint each factor by itself (kin communication, vocal imitation, slow reproduction, extended childcare, allomothering, tool use or flexible foraging) can be found in nonhuman species. It is only the combination of factors that appears to be unique to humans. However, the analysis here also directs our attention to several other groups of vertebrates which would seem to possess enough of the factors discussed above to warrant additional, open-minded investigation of their communication system. These include the corvids (the songbird family that includes crows, ravens, jays) and some odontocetes (toothed whales: dolphins, killer whales, sperm whales, etc). Both of these groups possess many of the characteristics argued here to be preconditions for the evolution of a language-like system (especially vocal learning, complex intelligence, and, in some corvids, both male and alloparental childcare). And in neither of these clades would it be safe to say that we fully understand the communication system of all species (or indeed of *any* one species, though the bottlenosed dolphin *Tursiops truncatus* probably comes closest, and shows no signs of

flexible semantic communication (Evans & Bastian, 1969)). Thus, although my primary goal here has been to synthesize the available comparative data, the hypotheses explored here also point the way to further comparative explorations of animal communication systems that might share certain key components of language, or provide examples of earlier stages of language evolution that currently remain conjectural. More generally, I hope that this discussion illustrates how an integrated comparative approach to understanding human evolution can provide important clues to the function, phylogeny and mechanisms involved in human language evolution.

*Acknowledgments.* I thank Gesche Westphal, Chrystopher Nehaniv and Caroline Lyon for comments on an earlier version of this manuscript.

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Emergence of Communication and Language

Lyon, C.; Nehaniv, C.L.; Cangelosi, A. (Eds.)

2007, XI, 438 p. 89 illus., Hardcover

ISBN: 978-1-84628-491-5