

The Fate of the Third Chimpanzee

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Session 4

Co-operation Revisited

I.**Introduction**

In the last three sessions, I have sketched a model of hominin evolution in which the evolution of co-operation is central to the transformation of hominin intelligence. Its evolution and elaboration profoundly re-shaped hominin developmental environments. Young hominins increasingly developed in worlds re-organised by previous generations physically, biologically and, most especially, informationally. And its evolution and elaboration profoundly re-shaped hominin selective environments. Information pooling, complex co-ordination and expanded technology selected for the cognitive capacities that distinguish us from our living relatives.

I argued in session one that one crucial element of this transformation was the evolution of a distinctive foraging style. Our ancestors co-operatively targeted high value, but heavily defended, resources. In my view, human economic life is anciently co-operative, for there is persuasive evidence that collective economic action and a division of labour is an ancient feature of hominin lifeways. In the distant past, meat consumption became a key part of hominin diets, probably via increasingly aggressive scavenging as a precursor to actual hunting, and it did so long before there is evidence of high velocity projectile weapons. If the impressive Pleistocene predators were dispossessed of their kills by volleys of thrown “handaxes” and/or stone-tipped javelins, we can safely assume that this was not a solitary (or even a small group) activity. Late hominins evolved a distinctive foraging style: it was information-rich, co-operative, tool-assisted, and it targeted high value resources. Both *sapiens* and Neanderthals depended on animal resources that could only have been captured by bands acting co-operatively. That suggests that collective foraging dates back at least to the last common ancestor of the two most recent hominin species. Both species have been successfully hunting large game for hundreds of thousands of years. Thus Martin Jones begins his Feast with a vivid account of the collective consumption of a horse kill site at Boxgrove, England, dated to about 500,000 bp . But without the ability to kill at a distance, large game can be taken only by groups acting together.

In session three, I explored the ways economic co-operation was linked to, and dependent on, an informational commons. We are obligate, habitual, inveterate and adapted social information pumps, sucking information and expertise from our social partners. In the last session, I explored the evolution and stabilisation of this informational commons. But humans also co-operate reproductively, not just economically. Human life history evolution has resulted in children who are long dependent on their adult protectors. Intergenerational resource transfers are a persisting and entrenched feature of human life. Children throw a long resource shadow over their mother's future; Sarah Hrdy estimates that it takes 13 million calories to raise a child from birth through to full independence. But though human children are very expensive, mothers do not bear the full burden. Human fathers invest in their children, providing some mix of protection, resources and direct care. Older siblings also often contribute to the family economy, again through some mix of provisioning and direct care of young siblings. This broader network of support is reflected in a striking difference in weaning. Despite the long dependence of human children, they are weaned early, on average between 2 and 3. Chimps wean at about 5 years; orang-utans even later.

According to Kristin Hawkes, Nick Blurton Jones and Frank O'Connell, grandmothers are the most distinctive element in the network of reproductive co-operation. Menopause is a very unusual feature of human life history: many women live for many years as active and competent agents after the birth of their final child, and these active grandmothers often play an important role in the care of their grandchildren. Chimpanzee populations do not have this demographic profile. Chimps do not live as long as people, and female chimps do not have long and active post-reproductive lives. Hawkes, Blurton Jones and O'Connell argue that this feature of human demography is not just distinctive, it is critical. Reproductive co-operation was the foundational form of human co-operation, and grandmothers were the critical adaptive breakthrough in the evolution of the distinctive form of human reproductive co-operation. The key player in the network that supports a mother is her very own mother.

Thus Hawkes, Blurton Jones and O’Connell articulate a conception of the evolution of co-operation which makes reproductive co-operation central, and which makes the role of grandmothing central to reproductive co-operation. They are sceptical about the idea that hunting is economically central to hominin evolution. And they are sceptical about the idea that the informational demands of the foraging life style shaped hominin evolution. In this session I aim to respond to these critical ideas. More importantly and constructively, I aim to integrate reproductive co-operation with the co-operative foraging model. In the next two sections, I outline the Grandmother Hypothesis and suggest that a modest version of that hypothesis can be integrated with the social foraging model that I have been developing. Sections 4 and 5 are about hunting and its role within foraging life. I argue that the data — even the contemporary data — fit the idea that hunting is a cognitive demanding, co-operative, core economic activity of foraging life better than those data fit Hawkes, Blurton Jones and O’Connell’s sceptical alternative. So I aim to synthesise a picture of reproductive co-operation with a more traditional ecological model of the co-operation revolution, but in a context which emphasises the general role of niche construction and cultural inheritance in human evolution.

II.

The Grandmother Hypothesis

For Hawkes, Blurton Jones and O’Connell the pivotal member of the hominin lineage is *H. erectus*. For while the evolutionary changes that resulted in modern humans took place gradually and over a long period, one can see *erectus* evolution as the time hominins became human. For *erectus* was the first of the out-of-Africa hominins; the first species in our lineage to expand geographically and ecologically. Its anatomy became human. *Erectus* hominins were our size; fully bipedal; large-brained; sexually dimorphic to a similar degree. Perhaps they also evolved towards *sapiens* life history patterns, with a lengthened lifespan and a longer period of juvenile dependence.

Hawkes, Blurton Jones and O’Connell take as their point of departure these life history patterns. In comparison with chimps and our presumptive common ancestor,

we are longer-lived, larger, and our children are dependent much longer. According to their grandmothering view of hominin evolution, children are not children for so long because of their learning needs. They are children for so long because they need a long time to grow a large body. Hominins could afford that time because adult mortality dropped. The grandmother hypothesis depends here on a model of life history evolution that begins with the idea that when all else is equal, selection will favour larger body size. But typically, all else is not equal. Size has to be paid for by delaying maturity, and delay is inherently risky. If the parents are at high risk of dying before their offspring are independent, or if the offspring are themselves vulnerable, that risk is too great. For many animals, the adult survival rate is too low to allow organisms to risk long juvenile periods and a slow growth to adulthood. They are likely to die before they recoup their investment in growth. But if there is a decrease in mortality rates, so risk falls, organisms can invest in size, delaying maturity. If the risk of extrinsic death is lowered, it is also worth investing in anti-aging physiology. For the rate at which an animal ages is itself variable. So we should expect to see positive correlations between long lifespans; large body size; delayed sexual maturity.

Hominins fit this basic pattern: we are primates with long lifespans, delayed maturity, and large body sizes. However, we contrast with other large-bodied long-lived primates in that females often have a long, active & healthy post-reproductive life. Women abandon direct reproductive effort, often long before they die. Why? According the Grandmother hypothesis, active post-reproductive women are an evolved response of the *erectus* lineage to the decreased risk of adult mortality, whilst living in increasingly seasonal environments. The reduction in mortality indirectly extended time as a juvenile via selection for increased adult size and thus delayed maturation. So children stayed children longer. Yet they needed more care, for in dry seasons children could not gather their own resources. As intensified climatic variation increased the seasonality of *erectus* environments, the hominin lineage faced a choice. Find dry-season resources and a way of delivering them to the young, or retreat to less seasonal refuges.

Washburn's hunting hypothesis was one candidate solution to this dilemma: meat and marrow are available in the dry season, and adult males (especially) deliver these

resources to women and children in extended family units. Hawkes, Blurton Jones and O'Connell have another suggestion: underground storage organs are the dry season resource, and (in fortunate families) an active grandmother finds and delivers these resources to the older children of her daughter. This allows those daughters to care for their infants, thus reducing the interbirth interval of families with active grandmothers. Towards the end of a life, the prospects for success, even for an active grandmother were low. Selection would thus favour both a late-in-life switch of female strategy from direct reproductive effort and investment in anti-aging physiology. The idea is that fairly modest periods as an aiding grandmother would be visible to selection, so active grandmaternal life could evolve (once extrinsic risk declines) by degrees. To improve her direct fitness, a potential grandmother going it alone as a late-life mother would have to survive as a competent agent through the whole period of the dependence of her final child. To improve her indirect fitness she might need only to take care of one three year old through one dry season, thus enabling her daughter to squeeze an extra infant into her lifetime fertility schedule.

So conceived, the grandmother model has five key components. It requires (i) a reduction of extrinsic mortality; this made delaying maturity profitable and opened the door to profitable investment in slowing aging. (ii) That reduction in mortality took place in environments which were increasingly seasonal, hence weanlings could not support themselves year-around by their own foraging. (iii) In dry season environments, late-mature women could generate a nutritional surplus; they could feed both themselves and a daughter's dependent child. (iv) The social organization does not force girls to leave the group of their birth. For the model to work, mothers must live in the same group as their reproductively active daughters. Moreover, they must be able to recognise their grandchildren. The recognition requirement is not trivial. For some fraction of mothers would have sons as their only adult children, and there are many breeding systems in which males cannot track their offspring. (v) Hominin populations contained a reasonable proportion of older adults: the strategy of abandoning direct breeding effort in favour of grandparenting can invade in reasonable numbers, making the linked behavioural and physiological dispositions visible to selection.

III

A Modest View Grandmothering

Some of these assumptions are quite credible. Hawkes, Blurton Jones and O'Connell themselves are most concerned to defend the demographic assumption: that there actually were grandmothers in ancestral populations in reasonable numbers. It is often suggested that long life expectancies are the privilege of modern populations. Populations of humans in traditional societies, and even more still more ancient populations, rarely contained the old in significant numbers. Not so, according to the Grandmotherers. They argue that there is independent evidence that long human life spans have a deep history. Ethnographic evidence of foraging peoples shows that such populations include significant numbers of post-reproductive adults (often about 20% of the adult population is over 45). Against this, there are paleodemographic studies that seem to show that ancient populations lack old survivors. But these might be the result of preservation biases. Older folks' bones are less likely to survive in skeleton assemblages than younger ones. So the Grandmotherers suggest that the basic pattern of *sapiens* seems to be essentially stable over forager-agriculture-urbanisation transition, despite real changes in fertility and life expectancy. Post-reproductive adults may be significant fraction of a population, even when the average life expectancy is in the 30s or early 40s. For such averages are compressed by large numbers of early deaths. So even if at-birth life expectancy approximates 40, helpful grandparenting will be visible to selection.

These considerations seem persuasive, so I agree that the demographic foundations of the model are credible. Likewise, the idea that reproductive co-operation is a central component of human co-operation is plausible. In many cultures, mothers have shorter interbirth intervals than chimps, even though humans are subadults for much longer, and even though weaned human children, but not weaned chimps, need not just food but a host of other resources too. These include shelter, clothes, protection, social support and education. We should not forget the costs of informationally engineering children's learning environments. *Erectus* children would have required some of these extra resources too. Higher cost children plus shortened interbirth intervals signals reproductive co-operation. However, grandmothering was probably

only one element of reproductive co-operation. Older siblings and aunts are often important in *sapiens* social worlds. So too are fathers and paternal relatives. There is no reason to suppose that these alternative channels of alloparental support have more recent origins than grandmothing. The extension of subadult life made older siblings available as potential sources of protection, education and support for longer. Moreover, siblings are as closely related to one another as mothers are to their children, so an aging female abandoning direct reproduction can gather as much indirect fitness benefit as an aunt as she can as a grandmother. That was especially true of daughterless mothers with sons. So aunting is as likely as grandmothing to be important. And while I accept that in ancient hominin social worlds, many mothers would still have had their own mother alive, many would not. As Hrdy points out, even on optimistic assessments of survival, only about 50% of mothers would still have their own mother. On other estimates that falls to about 25%. If allomothering was virtually essential for successful reproduction by earlier hominins, there must have been much allomothering that was not from the grandmother.

Moreover, there are tacit features of the model that imply that the evolution of grandmothing took place in a social environment that was already co-operative. The model assumes that the social environment is benign. Most underground storage organs cannot be consumed on the spot; they need to be processed. Moreover, they are often quite sizable packages of food. In a Hobbsian social world, grandmothers and infants with such resources would often lose them, and not just to occasional unfortunate encounters with the largest males. They would be vulnerable to junior and subadult males as well. In such social environments, the vulnerable need to adopt a feed-as-you-go foraging style, and harvesting and processing storage organs would not be viable. So the social environment must have been at worst passively co-operative.

Furthermore, the basic life history model on which the Grandmother Hypothesis depends connects the extension of the human lifespan to reductions in extrinsic mortality. This reduction was not the result of a more benign external environment. To the contrary, Rick Potts argued that the frequency and magnitude of environmental fluctuations increased in the second half of the hominin career. While Hawkes, Blurton Jones and O'Connell are silent on the reasons for the fall in mortality, the most plausible suggestion is that increasing co-operation reduced risk, by more effective defence against predation, and by dampening variance in food supply. Social

support through illness and injury might also have been important. Very basic nursing — providing food, water and protection — greatly improves the survivability of serious injury and illness. Finally, storage organs — supposedly the key grandmother resource — are rich. But finding them can be challenging and more crucially, as I have just noted, they often require complex cultural adaptations to process. Many are inedible without cooking, or washing and leaching to remove toxins. Such learned complex skills are a signature of information pooling and social learning; hence a signature of a social environment that has already shifted towards co-operation.

I conclude from these initial considerations that a modest version of the grandmother hypothesis is plausible. Grandparent-based reproductive co-operation was probably one part of the co-operation revolution in human life. But I am sceptical of the more ambitious idea that the evolution of the nurturing grandmother was the key innovation — the adaptive breakthrough that drove the hominin transformation. Grandmothering evolved in a milieu of other forms of co-operation; both reproductive, informational and ecological. It was part of an evolving co-operation suite; perhaps not even an especially central element in that suite.

IV.

Foragers: Ancient and Modern

On the social foraging model of hominin evolution and human subsistence economies, hunting is primarily an economic activity. It is important enough for the cognitive demands on hunting to reshape hominin life history. It is profitable enough to fund life history re-organization. Adult life is delayed, and cross-generational resource flows organised because this high-expertise foraging mode is very profitable. Adult foragers, especially males, deliver rich resources. But the expertise necessary to generate this profit takes many years to acquire. Childhood is an adaptation to the extensive demands of social learning; it can be afforded only because that learning makes adult activity far more profitable than it would otherwise be. The costs of learning are worth paying, because adult provisioning, especially adult male provisioning, is much more profitable as a result of this investment. Hunting is not the only foraging activity, nor the only one demanding skill, technology, information. But it is a core activity. In contrast, the Grandmother Hypothesis takes hunting to be

primarily a display activity. Hunting is advertisement and status competition, and long childhoods are a side-effect of the extension of adult life, and of the selection for increased adult body size.

Modern foragers loom large in this debate. Their lives have been used as a lens through which to interpret the remains of ancient lives. Yet there are profound differences between ancient and modern foragers. Despite these differences, modern data are indeed relevant, but as a conservative test of the social foraging model. I shall argue that the ancient to modern transition biases the data against the social foraging model and in favour of the display model. Despite this, on the whole the contemporary data fit the social foraging model better than they fit the display model. I conclude that the social foraging model fits ancient foragers better still.

Foragers and their world has been transformed over the last 150,000 years. One important transformation has been in the environment of co-operation. Maintaining stable co-operation has become more problematic. I claimed in session 1 that humans extract resources from their environment in a unique way: via collaborative expertise. Foraging is both co-operative, and dependent on expertise and technology. Ancient *sapiens* specialised in ungulates, but over the last 40, 000 years, the pattern of collaborative foraging has changed markedly. The broad spectrum revolution involved, inter alia, a shift away from larger game to small and medium size game, and to marine and other resources. The broad spectrum revolution selected for specialisation as different techniques and technology are needed for hunting, say, rabbits rather than wildfowl or fish. It also selects for much more small group and individual hunting. At the same time, this shift reduced both variance in daily success and average package size. Kills were much more frequent, but much less was provided per kill. In many environments, hunting became less collaborative, and the need for reciprocal sharing less pressing.

This social effect of the broad spectrum revolution was intensified by the projectile revolution. For perhaps the first 200,000 years of hunting and bully-scavenging, tool kits were simple and weapons fairly short-range. If humans between 200,000 and 40,000 had regular access to the meat of large animals, either by direct kills and by expropriating the kills of other large carnivores, technique and co-operation must

have been crucial. Between (perhaps) 30,000 bp and 20,000 bp, humans added spear throwers, bows & arrows, and poison darts to their arsenal. These changes make co-operation less critical. It became possible for individuals or small groups to kill large animals in relative safety. Large groups that hunt and kill together can share on the spot. There may still be a problem in controlling a greedy bully who wants to take more than his share. But the profit of joint activity is accrued together and in full view of all, so there are no informational problems in policing co-operation. If everyone is a roughly equal partner in a joint activity, it is much easier to see what is fair. The same is not true once individual success become highly variable (as individuals hunt alone or with favoured partners); once the range of resources expands (making commensurability an issue); once reciprocation extends over time. Moreover, vigilance becomes an issue once individuals spend much of their time, and enjoy much of their success and failure, away from the eyes of the many. Co-operation, all else equal, is most stable in small, homogenous groups. Increases in group size, heterogeneity and role differentiation made co-operation more difficult to manage, as the cognitive challenge of monitoring fairness becomes more pressing. I conjecture that co-operation became more fragile, and that the developing archaeological signature of ritual and public symbol use over the last 100, 000 years is a response to this fragility.

There has also been a transformation in the cognitive demands on a forager's life. In some respects, those may well have increased through the broad spectrum revolution and the expansion of material culture. For instead of having to have a detailed understanding of a few key target species, broad spectrum foragers had to have a feel for the natural history of many. Instead of having to master the techniques of producing a limited toolkit, they had to master the production of a much more varied technology. More recently still, some cognitive demands have become less onerous. The use of dogs reduces the pressure on tracking skills. Projectile technology makes concealment and stalking less difficult. Crucially, though, many foraging peoples have now supplemented or replaced home-built technology with store-bought equipment. As a consequence, empirical measures of learning all focus on foraging itself, rather than on making the equipment to forage. At best they measure only one aspect of the skill set of ancient foragers.

Finally, the economics of hunting have changed, dampening down the differences between male and female activities. The broad spectrum revolution has made much male hunting more like gathering. Those who target small game are exposed to less variance, and face less physical risk. It has become more of an individual activity, with less communally shared. Very likely it has a lower rate of return per hour of effort, for the revolution was forced by a decrease in encounter rates with the most desirable targets. With the massive depletion in most habitats of medium and large herbivores, hunting by contemporary and near-contemporary foragers is probably much less profitable. They live in a more Malthusian environment. The human footprint on the local resource profile has been heavy, persistent, depleting. Hunttable resources are less abundant, and those that remain are targeted by more.

While the male contribution shrank, women's and children's foraging may have become more valuable. In favourable circumstances, children can contribute significantly to the family economy. However, their contributions to the family economy often depend on technology and information which adults provide. Moreover, in most environments there is seasonal variation, so there will be parts of the year when resources are too hard for children to extract. So children are still not self-sufficient. But in many environments children's semi-independent foraging is possible only because predators have been largely eliminated, and those that survive have learned to avoid humans. This is probably a relatively recent Holocene development, one that has eased the energetic demands of children on their parents. To a lesser extent, the same may be true of female gathering. If we set aside the threat from other humans, this is surely much safer than it was 100,000 years ago, when we were one of an impressive set of African Pleistocene predators.

Thus contemporary and ancient foragers did not face similar ecological, social and sexual decisions with similar resources. Ancient hunting was probably more routinely co-operative, with large kills shared on the spot amongst quite large hunting parties. The most available prey was more abundant both relatively and absolutely, and so the profit of hunting was probably higher. Gathering by women and children may well have been somewhat constrained by predation threat. Ancient hunters had to manufacture all their own equipment; detect and get close to their prey; track prey with their own observational powers rather than piggyback on those of dogs. So if the

results of hunts are still regularly shared; if hunting is more profitable to hunters and their family than gathering; if foraging in general and hunting in particular is highly skilled, where older and more experienced hunters still do better than young adults in their physical prime, then we can extrapolate these traits, and then some, back to ancient foragers. What though of the display model? How well does it fit contemporary foragers? To that, I now turn.

V

Hunting: Provisioning or Signalling?

Costly signalling models apply to signal systems in which agents signal about themselves, trying to induce others to act to the signaller's own benefit. The crucial idea of costly signalling is that agents have an interest in advertising their high quality, but that less fit agents have an interest in overstating their quality. Costly signals enable the audience to discriminate between high quality agents and pretenders, because the signals are not just costly; they are differentially costly. Frauds cannot afford the signal, and so its reliability is stabilised by the differential cost of sending it.

Hawkes, Blurton Jones and O'Connell suggest that large game hunting (in particular) functions to send a costly signal. Hunters advertise their quality. Hunting, the idea goes, is an unfakable signal of quality: only the genuinely fit hunt successfully. Despite its popularity, I think this model is quite unpersuasive. We should expect costly signalling to be an individualistic activity: as is, for example, building a new art gallery for a city. But this does not fit the pattern of hunting in many forager societies. Even in contemporary times, hunting is often collective and co-operative rather than individual. The Lamalera's co-operative hunting of sperm whales is one contemporary foraging example. Moreover, as I argued in section 3, only the invention of penetrating projectile weapons made individual and small group large game hunting possible. Such technology is very recent. In Frank Marlowe's recent review, he dates spear-throwers to about 17,000 years ago; bows and poison to around 11,000 bp. Yet there is persuasive evidence that large game hunting played a central role in

human economies long before these dates. So hunting became central to human life as a collective, co-operative activity.

We expect sending costly signals to be not just individualistic; it should be a minority activity. For the costly signal is a display of unusually high quality. So on the costly signal model, we would expect only the expert to hunt and share. Poor hunters should keep what they catch and scrounge what they can. Perhaps more likely, they should abandon hunting altogether and forage like a girl. If hunting-and-sharing genuinely is individualist signalling for individual advantage, drop-outs need not fear being excluded from the distribution of product. They are not defecting from a co-operative activity. Others should welcome their withdrawal from competitive signalling. Hunting should be like playing baseball in America: the best hunt, and the rest watch. But this does not fit forager ethnography. In many cultures, males are notoriously addicted to hunting. So on costly signalling models of hunting, hunting and sharing by the less expert remain unexplained.

It is true that costly signalling is a natural model of some forms of prosocial behaviour in human life: bigman feasts; conspicuous gift-giving to charity; perhaps supererogatory displays of courage in inter-communal conflict. And there do seem to be examples of male hunting which fit the signalling paradigm. A persuasive example is that of Meriam turtle hunters. A crucial fact about the Meriam is that not all the males hunt (and few are hunt leaders). Moreover, turtle hunting does not seem to make sense as an economic activity. There are alternative, and more rewarding sources of protein (and, in the right season, even of turtle meat). Successful catches are shared, with no evidence of family bias or reciprocation. Finally, there is evidence that turtle hunters are fitter. They have a higher reproductive success, both because they acquire mates earlier than non-hunters and because they have higher-quality mates. So the idea that turtle hunting is a successful and reliable signal of high quality is plausible.

So some contemporary hunts probably are signals. But can we generalise from this example? The data are patchy, but the Meriam seem to emerge as the exception rather than the rule. For while the Meriam turtle hunters do not seem to share with their

group in expectation of reciprocation, nor use their catch to preferentially provision their families, Michael Gurven and Kim Hill argue that this pattern of sharing is exceptional. Hunters typically have considerable influence on the distribution of their hunting profits, and that these influences result in a bias towards kin (as a provisioning model would predict), and towards those that reciprocate. Food is given to those that give. To the extent that male sharing is contingent on others' response, sharing large catches seems likely to be a variance reduction strategy.

Moreover, hunting does seem to be a relatively efficient form of provisioning. In some environments it is mandatory: high arctic foragers must hunt. In less extreme environments, there are other options. But while few studies are detailed and quantitative, several show that male hunting generates an average rate of return per hour of effort of around twice that of gathering. And calorie counts understate this difference: meat is much richer in reliable macronutrients (proteins and lipids) than vegetable based foods.

Indeed, Gail Kennedy uses such nutritional facts to argue that reproductive cooperation could not be based on plant-based resources like storage organs, as the Grandmother Hypothesis suggest. She points out that growing children need very specific resources. Weaned young children need more than calories: they need protein to fuel their post-birth brain growth. For earlier hominins, scavenged brains and bone marrow are the most plausible source of these protein needs, and such scavenging is unlikely to be a grandmaternal speciality. The early age of human weaning has serious costs: weanlings have a higher exposure to pathogens at an age where their immune system is less well-developed, and when they lose the indirect immunological benefits of mothers' milk. The Grandmother Hypothesis assigns the benefits of early weaning to mothers. Early weaning, supported by allomothering, reduces the interbirth interval and increases lifetime fertility. Kennedy thinks the compensating benefits derive from the child's need to fuel post-birth brain growth, given the unsuitability of maternal milk to fuel that growth once children are roughly of weaning age. So the benefits accrue to infants. They avoid the protein gap (driven by brain growth) that would open out as protein needs increase beyond the point that they can be sustained by maternal milk. If this nutritional argument is sound, hunting

and male support for female reproduction is more important than a mere calorie count would show.

So there is a good case for thinking that hunting is an especially profitable form of foraging, and a good case for thinking that it was once still more profitable. There is some case for thinking that it was essential, once hominins evolved large brains. But even if on average, hunting is no more productive than gathering, specialisation in different resources will generate synergies when the family unit needs a variety of resource and when each resource can be gathered only by those with special skills and/or equipment. Moreover, we do not need to suppose that women are constitutionally unable to hunt for the sexual division of labour to be stable. Initially small symmetry-breaking differences followed by a positive feedback loop can lead to stable differences between the genders. Finally, while it is true that returns for male hunting are more variable than those of gathering, it certainly does not follow from that that the economically rational, family-provisioning male would gather rather than hunt. There is significant variance with gathered resources too, and the negative impacts of variance can be reduced. Storage, sharing with other hunters, hunting small game and female gathering itself all reduce the negative impacts of variation in hunting success.

In short, the transition from ancient to modern foraging is likely to have improved the fit of the signalling model with the data rather than eroded it. But even when we focus on contemporary foraging, the model fits the general trends rather poorly.

VI

Finale

On the Hawkes, Blurton Jones and O'Connell model of human evolution, increased seasonality is the key to the evolution of human co-operation. In so far as the evolution of human co-operation had an external, extrinsic trigger; that is, in so far as it was an evolutionary response to a change in the selective environment that occurred independently of human impact, I am inclined to agree. But that agreement comes with three caveats. First, I suspect that increased seasonality selected for ecological as

well as reproductive co-operation. In particular, given that Pleistocene Africa boasted an impressive stock of predators; given that increased seasonality turned hominin habitat into savannah and woodland with much less natural cover than forest; and given that early hominins were not physically imposing, selection for effective response to predators would have been strong. So my best guess is that collective defence was an early and important element of the co-operation syndrome. Second, I think this process began (as did increasing seasonality) earlier than the evolution of *erectus*. The habilines used simple stone tools, and while the capacity to make and use stone tools may well not require high fidelity cultural transmission, it will have depended on some form of hybrid learning; perhaps socially primed trial and error learning. Some form of information pooling was beginning to characterise habiline life.

Finally, while the expansion of hominin co-operation may have required an initial extrinsic trigger, its origins altered the selective and developmental environments in ways that selected for further co-operation. The evolution of human co-operation was largely driven by positive feedback. I have conjectured that co-operative defence, perhaps using thrown stones was a very early form of hominin co-operation. Successful collective defence preadapts for further co-operation; in part by reducing mortality and selecting for the life history changes that make advanced social learning possible. But it also makes collective scavenging and access to predator's kill sites possible. Furthermore, it pre-adapts hominins psychologically and socially to the collective suppression of dominant, expropriating males, thus opening the door to collective foraging, central place foraging and (more generally) variance reducing strategies that rely on trust and secure possession of one's resources. On this picture; there is no key adaptation or magic moment, Rather, human uniqueness depends on the evolution and stabilisation of a set of positive feedback loops which connect technology and the division of labour with co-operation, with social learning and with informationally engineered developmental environments. We are creatures of feedback.