Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess

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Geographical cataloguing of traits, as used in human ethnography, has led to the description of ‘culture’ in some non-human great apes. Culture, in these terms, is detected as a pattern of local ignorance resulting from environmental constraints on knowledge transmission. However, in many cases, the geographical variations may alternatively be explained by ecology. Social transmission of information can reliably be identified in many other animal species, by experiment or distinctive patterns in distribution; but the excitement of detecting culture in great apes derives from the possibility of understanding the evolution of cumulative technological culture in humans. Given this interest, I argue that great ape research should concentrate on technically complex behaviour patterns that are ubiquitous within a local population; in these cases, a wholly non-social ontogeny is highly unlikely. From this perspective, cultural transmission has an important role in the elaborate feeding skills of all species of great ape, in conveying the ‘gist’ or organization of skills. In contrast, social learning is unlikely to be responsible for local stylistic differences, which are apt to reflect sensitive adaptations to ecology.

Keywords: animal cultures; social learning; cognition; behavioural complexity; technical intelligence

1. INTRODUCTION

Biologists usually become interested in animal culture for one of two rather different reasons. On the one hand, their concern may be directly with the ‘second inheritance system’ (Whiten 2005) that social learning potentially offers: what information is transmitted; how fast it spreads; what environmental features slow or block transmission; how this information interacts with genetically coded information; and so forth. For these purposes, the starting point is to identify clear cases of social transmission, either by experimental interventions (e.g. removal or translocation of knowledgeable individuals) or by a pattern of spread that is distinctive of social transmission (e.g. a historical record of the relatively rapid, monotonic spread of a habit, checked by major environmental barriers). Ideal species to use are ones that are common, widely distributed and easily manipulated, such as garden birds or reef fishes. Ideal traits for study are those that are relatively unrelated to the local features of the environment, such as habits of social behaviour or display.

On the other hand, biological interest in animal culture may derive from culture’s privileged status as (putatively) uniquely human and from its role in human technological superiority over other species. As with all claims of uniqueness, human technology holds out a challenge to the biologist to find the

evolutionary origins of the unique human pattern. In this case, we might expect interest to have focused chiefly on behaviours that clearly involve technological skills but are found in non-human species, in particular the closely related great apes. This article will make the case that, in fact, these two different approaches have become mixed together in their methods and that this risks impeding a biological understanding of the origins of human technological culture.

2. CULTURE IN GREAT APES: PATTERNS OF LOCAL IGNORANCE

Begun nearly 50 years ago, the systematic observational field study of the chimpanzee soon revealed striking behavioural variations from one site to another: in diet; in manual feeding skills including tool-use; and in social signals (Goodall 1963, 1973; Nishida 1973, 1980; Sugiyama & Koman 1979). More recently, some of these differences have been described as constituting *culture* in the chimpanzee (McGrew 1992; Whiten *et al.* 1999), with a similar argument made for the orangutan (van Schaik, *et al.* 2003) and the bonobo (Hohmann & Fruth 2003). These claims, based as they were on very extensive fieldwork, generated considerable interest and excitement: not surprisingly, when for so long culture has been considered a hallmark of our own species, unique and inaccessible to analysis by the comparative method.

The identification of great ape culture has been based on patterns of behaviour, ‘transmitted repeatedly through social or observational learning to become a population-level characteristic’ (Whiten *et al.* 1999),

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forming 'a system of socially transmitted behaviour' (van Schaik *et al.* 2003). However, because apes are long lived, and because even the most intensive field study is insufficient to trace ontogeny in detail, social learning was diagnosed retrospectively, by excluding alternative explanations. Field experiments involving translocation or removal are simply not feasible with endangered and rather large animals in remote locations of Africa. The approach taken in the recent 'ape culture' papers has been to focus only on traits that showed a pattern of site-to-site behavioural variation, on the grounds that universal behaviours could be more parsimoniously explained without reliance on social learning. The idea is that any behavioural differences between sites that can be satisfactorily explained by genetic variations or by ecological difference should be set aside, and then those traits that remain can be safely considered to be cultural traditions. This procedure is a conservative one, and clearly risks excluding behaviours that are in fact socially transmitted but have already spread to universal coverage, or whose patchy distribution correlates with ecology because their function is ecological (Perry & Manson 2003).

In the case of the chimpanzee, 42 behavioural traits were considered to be customary or at least habitual (i.e. 'has occurred repeatedly in several individuals') in one or more communities but absent in one or more others (Whiten *et al.* 1999, 2001). These candidate cultural variants were then pared down by exclusion. If a trait differed systematically between two genetically separate populations, such as the subspecies *Pan troglodytes verus* and *Pan troglodytes schweinfurthii*, but was found universally within each population, it would be ascribed to a genetic difference. In fact, none of the behavioural variants examined in chimpanzees were set aside on such a basis (although, in fact, evidence of nut-cracking is found entirely within the two western subspecies of chimpanzee, *Pt. verus* and *Pan troglodytes vellerosus*, and variation across Africa in chimpanzee nut-cracking might thus have been attributed to genetic causation). Conversely, if the distribution of a behavioural trait correlated closely with some relevant ecological variable, it would be ascribed to ecological determination. Three of the behavioural variants were considered 'explicable by local conditions': scooping algae with a stick; making night nests on the ground; and using a rock to level an anvil. The 39 remaining patterns were identified as cultural variants for the chimpanzee: for the orang-utan, the corresponding figure was 24 (van Schaik *et al.* (2003); however, in five of these, the variation was noted to be potentially explicable on ecological grounds.

The logic of this process is that the remaining behavioural variations must result from limitations on knowledge transmission. Invention is a rare event (or else all apes would be able individually to acquire the skills), but social learning allows knowledge to spread within the social network, within and sometimes between social communities; spread is limited by breaks in the social network caused by natural barriers. Outside the network of privileged knowledge, apes will remain in ignorance, or may acquire a characteristically different behavioural variant by virtue of membership of another social network in which a different technique

has been invented. In short, by means of cultural transmission, apes are able to acquire beneficial abilities that they would otherwise lack, but imperfections in social transmission impose a distinctive variation from optimality. Evidence that large rivers *can* sometimes constitute barriers to knowledge flow comes from chimpanzee nut-cracking (Boesch *et al.* 1994; McGrew *et al.* 1997) and orang-utan *Neesia* eating with tools (van Schaik & Knott 2001); across the rivers, the same potential foods are present, but remain unexploited.

Most strikingly, a single important chimpanzee foraging technique, ant-dipping, was found to vary in behavioural *style* rather than merely presence, with resulting effects on efficiency. The two-handed method used at Gombe, East Africa, was estimated to be four times as efficient, in ants/minute, than the one-handed Tai, West African equivalent (McGrew 1974; Boesch & Boesch 1990). The cultural explanation is that ant-dipping must have been invented at least twice, but different ways of achieving the purpose became stable in different knowledge networks. Despite the dramatic difference in efficiency, behaviour did not converge on the optimal form, but continued to conform to the socially learnt original: 'Tai chimpanzees restrict themselves to the suboptimal solution that must be maintained by a social norm' (Boesch 1996). Researchers concluded that 'it is difficult to see how such behaviour patterns could be perpetuated by social learning processes simpler than imitation' (Whiten *et al.* 1999); and they postulated that the more complex technique derived culturally from the simpler method by 'differentiation in concert with diffusion, a process more deserving of the term "cultural evolution"' (Whiten *et al.* 2001).

Detection of ape culture, then, has been based on identification of local ignorance (Byrne *et al.* 2004). The biggest difficulty in ascribing ignorance is of that of conclusively ruling out all alternative ecological explanations (Tomasello 1990, 1994; Galef 1992), and this is a significant weakness in the approach. Whiten *et al.* (2001), for instance, consider invulnerable to ecological explanation those variations in plant-based behaviours that 'depend on leaves or other simple configurations of vegetation, of which many different kinds appear suitable for the task'. Yet, until the properties of the key plant materials have been compared between sites where they are or are not used, such claims will always be open to sceptical reappraisal. Slight differences in material that correlate with—and potentially explain—the behavioural variation may be missing simply owing to lack of detail on the identity and properties of plant material in the primary accounts. This is not hypothetical concern: major behavioural differences in the method used by West and East African chimpanzees to feed on *Dorylus* ants were overlooked for many years, despite the level of scientific interest in ape tool use. Ecological influences form a complex web of interconnections, many of which may currently be unknown, particularly in a species like the chimpanzee with its immensely varied diet and behavioural repertoire (Nishida & Uehara 1983; Nishida *et al.* 1999).

Of the 'cultural variants' in chimpanzees, 18 involve feeding on specific plants or animals, 21 employ specific plant material as the means and 2 involve removal of specific noxious insects. Taking these together, some ecological explanation for variation could be made in 32 of 39 cases, in addition to the three cases actually rejected as potentially explicable by ecology.

This concern is not merely theoretical: ecological differences in chimpanzee foods can be subtle. Mound-building termites are found at three study sites on the eastern shores of Lake Tanganyika, yet chimpanzees at one of them (Kasoje) do not use stems to fish for them. Collins & McGrew (1987) carried out detailed study of the termites and found that three different termite species of two genera were involved, concluding that the chimpanzees' behaviour matched the termite species available rather than reflecting cultural differences. More generally, the foraging ecology of the chimpanzee is little understood at any one site, and the site-by-site differences even less so. This has already become evident in the celebrated case of variations in ant-dipping style, initially discussed as a rock-solid case of cultural transmission, which are now known to depend significantly on ecological differences. Species of *Dorylus* ants vary from site to site, and at one location both methods have been found to be used by the same individual chimpanzees, for different species of ant and at different phases of the ant foraging cycle (Humble & Matsuzawa 2002). Rather than a pattern of patchy ignorance, it now seems that behavioural variation in ant-dipping, like that of termite-fishing, shows exquisite sensitivity to local task demands.

Of course, any innovative, large-scale research programme is likely to include occasional mistakes that need later correction, but there are reasons to think that the problems of separating ecological from cultural determination may go deeper in this case. The chimpanzee and the orang-utan are unusual in the richness of their known diet sets and behavioural repertoires, even among primates living in tropical forests. Yet neither has been subject to phytochemical and nutritional examination in the kind of detail needed to reveal subtle interactions among alternative diet items, nor study of the mechanical properties of material that may potentially be employed in tool use. This level of ignorance is unsettling in the context of a study method that depends on exclusion of ecological factors. Geographical comparisons can be telling where a particularly distinctive pattern is found: that of universal spread checked by a barrier, as for orang-utan *Neesia* eating. However, this distinctive pattern is the exception rather than the norm; for instance, in the chimpanzee only nut-cracking with hammer and anvil (West Africa) and intense grooming of leaves (East Africa) were found to be so (Whiten *et al.* 2001). Most locally varying habits are patchily found right across the chimpanzee range. It would seem that the traits identified as cultural are not difficult for chimpanzees to invent, and that invention has occurred independently at many sites. Still less, has any sign been found in non-human great apes of the pattern more typical of human culture, where a whole suite of differences co-occur between one group of people and another:

people who build pagodas are likely to use chopsticks to eat rice, people who build water turbines to grind barley are likely to show fraternal polyandry, and so on. In chimpanzees, there are no such 'packages' of correlated behavioural traits, and the level of behavioural difference is often as high between nearby study sites as distant ones.

With no opportunity for translocation/relocation experiments, no historical evidence of habits spreading across geographical areas and few patterns clearly implicating past spread by social transmission, the case for great ape culture rests on much weaker foundations even than that for culture in birds or fishes (Laland & Hoppit 2003). In the absence of these stronger types of evidence, patchiness of distribution does not necessarily signify culture. If a habit can be invented multiple times, perhaps it can be invented by every individual that has real need of it? This is evidenced by the fact that a number of 'chimpanzee cultural variants' have also been identified in the bonobo (Hohmann & Fruth 2003), not only a different species but also one separated from the chimpanzee by Africa's largest river; these include the grooming handclasp (see McGrew & Tutin 1978), leaf-clipping as a social signal, aimed throwing and fly-whisking with vegetation. The two ape species must both possess a propensity to invent and re-invent the same actions under similar circumstances. Given such a propensity, tracing which patterns of variation are in fact due to cultural transmission becomes difficult.

Finally, if most or all of the 'cultural variation' of chimpanzees is indeed a result of imperfect social transmission, the continued existence of the differences logically presents a puzzle (Byrne *et al.* 2004). Female chimpanzees regularly transfer between communities when they reach adolescence (Nishida & Kawanaka 1972), an age at which they should already possess the cultural knowledge of their natal community, thus making this knowledge available to at least the younger members of the new community. (In orang-utans, major barriers, including mountain ranges and seas, make isolation of knowledge more likely; in this case, the corresponding likelihood of isolated gene pools is more of a challenge to the identification of definitely cultural variation.) Over time, regular female transfer between chimpanzee communities means that very large areas of Africa have been until recently part of the same potential knowledge network. Yet the site-to-site variation in behaviour patterns charted by Whiten *et al.* (1999, 2001) does not, in general, follow natural boundaries to chimpanzee movement. Nor is there any sign that this situation is temporary; the differences are apparently stable and long lasting, over decades of study at several sites, in contrast to the rapidly changing cultural traits of capuchin monkeys (Perry & Manson 2003; Perry *et al.* 2003).

If a socially acquired trait is beneficial, or there is an optimally efficient way of carrying it out, this knowledge *should* spread between communities; local ignorance should only be temporary. If the behaviours concerned relatively trivial fads, not conferring any real advantage to their possessors, then their spread might be haphazard and it could be argued that a tendency to conformity (Whiten *et al.* 2005) could prevent

knowledge invading a geographical area of relative ignorance. This might be the case for some of the odder and less obviously functional variants, but if the ape cultural traits were found in general to be no more than fads, their interest to anthropology and zoology would decline. Thus, the stable but patchy distribution of apparently useful traits in the chimpanzee is itself something of a challenge to the idea that the variations result from cultural transmission.

3. AN ALTERNATIVE APPROACH: INTRICATE COMPLEXITY AND LOCAL UBIQUITY

The use of geographical patterning to identify culture in great apes is liable to lead to a trap. In human cultures, distinctive patterns of variation persist in non-Western societies owing to the relative slowness of change by human invention compared to the rapidity of cultural diffusion and owing to xenophobic social mechanisms. In non-human great apes, distinctive patterns are always more likely to derive from ecological fit; stable patterns of local ignorance seem improbable in a species that regularly transfers individuals between groups. This challenge forces attention onto traits with site-to-site variations that have no possible ecological correlates (or invites criticism from sceptics). Often, these are just the traits which are the least likely to give insights into the evolutionary origins of human technological cultures, because they are very simple actions or because their ecological impact is trivial. In the process, many real cases of socially learnt skills are potentially discarded, because they do not vary sufficiently or because they correlate with ecological factors. At best, the result is liable to be a heterogeneous collection of traits for which geographical variation is socially caused, but few of which have any relevance to the cumulative skills of human culture. To get out of this trap, and make a serious attempt at using great ape data to explain the evolution of human technological culture, a different method may be needed than ape ethnography.

Recall that the original reason for picking on traits that showed geographical variation, and then retrospectively ruling out ecological and genetical causes for some of them, was to identify which traits originated from social learning (given the non-feasibility of establishing this experimentally). The need for this process is indisputable for simple habits, easily picked up individually, as indeed are many of those discussed as potential great ape cultural variants. However, as the complexity of a skill increases, the likelihood of wholly individual learning decreases. Compare, for instance, the human traits of 'eat pistachio nuts' and 'raise water by making a shadoof'. Individual exploration and trial-and-error learning is just not likely to be the sole origin of an individual person's tendency to make a shadoof, and it would not be sensible to require the same degree of evidence for shadoof-making as a social tradition as for an easily learnt dietary choice. Of course, great apes make nothing as complex as a shadoof. But where the biological interest is to begin to understand human technological supremacy—resulting from the cultural accumulation of knowledge that underwrites a wealth of skilful abilities—it would seem to make sense to

focus first on just those activities that manifestly require some skill. For this reason, it should not be surprising that, even though there is very much better evidence in both rodents and fishes for local differences in behaviour that are firmly established to be a result of knowledge transfer by social learning (Helfman & Schultz 1984; Warner 1988; Galef 1990, 2003; Laland & Hoppit 2003), this work has nevertheless not led to comparable claims of 'rat culture' or 'fish culture'. None of these undoubtedly socially transmitted habits is closely relevant to the cumulative culture of human technology.

As van Schaik *et al.* (2003) note, culture—as they define it, local variation not obviously explained by ecology or genetics—may contain a number of very different sorts of information. At the most basic, this may simply concern whether something is edible or where females tend to be when spawning: such 'labels' are culturally acquired in a wide range of taxa. Going beyond mere labels, song dialects in oscine passerines also furnish clear evidence of culturally mediated patterning. These birds reliably acquire their species song by social learning, and what is learnt can then be termed a 'signal'. In contrast to these widely distributed kinds of culture, van Schaik *et al.* (2003) assert that the cultural transmission of *skills* is unique to orang-utans, chimpanzees and humans. If ape culture is worthy of special attention—beyond that accorded to cultural transmission processes in more easily studied species such as birds and fishes—then it is because great ape feeding ecology is reliant on complex skills that may need to be acquired culturally.

Many species of animal occasionally use a tool, and a diverse range of species are known regularly to use a single type of tool for a particular purpose (Beck 1980). But in many populations of chimpanzee, and one of orang-utans, the intricate series of actions involved in selecting, constructing and employing tools goes well beyond these minimal cases; one example from each will suffice to illustrate. Chimpanzee termite-fishing is not a logical response to the perception of edible insects. Indeed, the insects are hidden deep within termite mounds which have no visible entrances. The ape must know that at a certain season it becomes possible to pick open a hole in certain places. In fact, this is only possible above what will later become the nocturnal emergence tunnel for the sexual forms of the termites, so the chimpanzee must also know how to recognize a sealed exit. Only when a suitably long, thin and flexible plant stem is inserted slowly through this entrance (and sometimes the plant stems are picked, stripped of leaves and bitten to a standard length, in advance of arrival at the mound) can it be withdrawn with termites attached (Goodall 1986). Comparable skills are shown by orang-utans at Suaq, Sumatra, which make small tools by biting off a twig and stripping it of bark, then use it to scrape out the irritating hairs from a ripe, part-open *Neesia* fruit. When the hairs are cleaned away, the same tool is used to dislodge the seeds to eat (van Schaik *et al.* 1996).

These two examples are also, as it happens, geographically patchy, but in general local patchiness of distribution does not single out traits of manifest difficulty. Few of the dozens of reportedly cultural traits

of great apes involve any real skill, in terms of subtlety, complexity and likely difficulty of acquisition without a skilful model. Only hole-probing with tools in the orang-utan, and ant-dipping, nut-cracking and hole-chiselling in chimpanzees, in addition to the two examples already noted, require manifest skill. Conversely, geographical *uniformity* does not exclude social learning as critical for acquisition. Indeed, ecologically important skills that depend on social learning would be expected to spread steadily through the population until checked by a major natural barrier. Within in the ranges of the African great apes, natural barriers chiefly consist of great rivers, and the patchy distribution of behaviour traits does not map onto the distribution of rivers. Another criterion is needed to direct research attention to the most informative behaviour.

I propose that the combination of *intricate complexity* of behaviour, and *near-ubiquity* among a contiguous population, can be used as an alternative hallmark of culture in great apes. This criterion has the advantage of focusing attention on great ape behaviour that is in principle relevant to better understanding the origins of human culture—where it is the intricate patterns of complex action that have long impressed anthropologists. Intricately complex behaviour patterns are highly unlikely to be invented multiple times, making cultural transmission an essential feature of their widespread dissemination, and near-uniformity within a population points to the skills' importance for survival.

Removing the need for 'local variations without ecological correlate' opens the gate to a much wider range of great ape skills potentially acquired culturally. As noted above, ant-dipping by chimpanzees varies in style in ways that make good ecological sense as ecological adaptations to different ant species (Humble & Matsuzawa 2002), but this need not disqualify the behaviour itself as cultural. The elaborate series of skilled actions involved in ant-dipping is highly unlikely to be learnt by a solitary chimpanzee. Of course, many of the important details of how the job is done are likely discovered individually, as with any complex skill; it is most probably only the *idea* or *gist* of ant-dipping with a stick that is socially learnt. The same may apply to several other chimpanzee tool-using skills (e.g. nest construction, algae-scooping, leaf-sponging), not considered as part of chimpanzee culture, and to plant-preparations skills not involving tool-using, such as opening and eating *Saba* fruit (Corp & Byrne 2002). Almost all orang-utan populations lack elaborated tool use, but most show intricate, complex skills for dealing with plants, in particular to enable pith consumption from spiny palms and rattans (Russon 1998).

Using the alternative definition of 'intricate complexity and local ubiquity' allows great ape culture to be studied in other species where patchy geographical distribution would be undetectable with current data. Gorillas do not make tools in the wild, and only one population has been studied at the level of detail needed to detect complex skills in plant-processing. But several of their food-processing skills consist of highly structured, multi-stage sequences of bimanual action, hierarchically organized and flexibly adjusted to plants of highly specific local distribution

(Byrne & Byrne 1993; Byrne *et al.* 2001a,b); and these abilities are near-ubiquitous among the local population. In terms of intricate complexity, gorilla plant-processing actually *exceeds* anything yet described in chimpanzees, unless tool-use *per se* is taken to be intrinsically more complex than non-tool-use. *Gorilla*, like *Pan* and *Pongo*, apparently sometimes relies for its survival on elaborate, dextrous and intricate feeding skills that are highly unlikely ever to be discovered by a solitary individual (Byrne 1997, 2004). Since nothing of the kind has been reported in any monkey species, the underlying cognitive ability is likely to have a relatively recent (i.e. ancestral great ape) origin and relate directly to the origins of human technological superiority.

4. POSSIBLE CONCERNS

It could be argued that shifting the focus of ape culture research firmly towards behaviour of intricate complexity, rather than requiring geographical patchiness, opens the possibility of confusion with genetically determined traits or with behaviour that can be acquired without social learning at all. How serious are these concerns for great ape research? Many species of animal show intricate complexity of behaviour, most obviously in construction of nests, bowers and dams (Hansell 2005); and much display behaviour is also complex and highly patterned. However, such traits are far less evident for primates, species whose flexibility of repertoire and reliance on learning have always impressed researchers. Some of the most intricate great ape skills make no sense at all when viewed as genetical products. For instance, the plant-processing of mountain gorillas is so specific to plants of limited altitudinal range as to be valueless a few miles away from where they were recorded, yet the distribution of this species of gorilla extends for hundreds of miles.

Alternatively, it has been suggested that even the most elaborate skills of wild great apes could in fact be discovered by each individual separately, and would then be channelled towards near-uniformity in the population by the affordances of the hands and the natural materials involved (Tomasello & Call 1997). Whether or not this proposal is considered plausible, no evidence has yet been offered that it is correct; and several pieces of circumstantial evidence are against the idea. These include: (i) as discussed above, the complex skills of apes are occasionally distributed in a way that implies spread effectively blocked by natural barriers, (ii) apes that have suffered maiming from snare wounds to the hands in infancy nevertheless acquire the same techniques of skill as their able-bodied peers, rather than discovering different methods consistent with the very different affordances of their maimed hands (Stokes & Byrne 2001; Byrne & Stokes 2002), and (iii) while great ape skills show extensive individual variation at a detailed level and in handedness, as would be expected from individual accommodation to task demands, the overall structural organization seems to be universal in the local population (Byrne & Byrne 1993).

Working with natural data, no perfect method exists for the identification and study of cultural phenomena.

Defining ape culture on the basis of intricately complex skills that are near-uniform in a contiguous population has several advantages, however, over the use of geographical patchiness. Research focus is brought firmly to bear upon behaviours of ecological importance to the species concerned, which are in important ways 'like' those that underpin human cultural uniqueness. In particular, they are elaborately complex activities, exquisitely adjusted to solving practical problems, relatively obvious in broad outline 'once you see it', but unlikely to be discovered by an individual restricted to lone experimentation. Inter-population variations in behaviour may sometimes result from breaks in a knowledge network, and these cases are fascinating to study; more often, variation is likely to result from hidden ecological differences, especially in species whose ecology is not fully understood. Population uniformity of complex, apparently skilful behaviour may occasionally result from tight genetical channelling ('an innate trait'), and any cases discovered would be worthy of study; but none is particularly likely in a simian primate species. In general, intricate complexity, in a trait that is near-uniform in the population, signals culturally guided acquisition of an important survival skill.

5. POSTSCRIPT: MEASURING COMPLEXITY OF BEHAVIOUR

To apply this criterion, some way of measuring and comparing complexity across tasks is needed, as a way of estimating the likelihood of individual invention (thus 'complexity' is here used to include all aspects of the task that make learning more difficult). There are a number of possibilities. Mathematically, complexity can be measured as information (Shannon & Weaver 1949), and a simple way of estimating information content—by counting repertoire sizes—has been advocated for estimating the complexity of animal behaviour (Sambrook & Whiten 1997). Since any complex task will be composed of simpler building blocks, on this approach one would count the number of elemental 'building blocks' of behaviour involved in any task—and if the species carries out several complex activities, as in the case of some chimpanzee, gorilla and orang-utan populations, these actions can be summed to estimate the total 'skill relevant repertoire'. The feasibility of this approach was investigated for mountain gorilla plant-processing skills, defining as different actions those that differed in their visible form and movement patterns (e.g. precision holding with fingers 1/3 versus fingers 1/2). Significantly, more elements were found to be used when gorillas process leaves of thistle *Carduus* than those of bedstraw *Galium* or nettle *Laportea*, for a given amount of data (Byrne *et al.* 2001b). For this one thistle species, in processing both stem and leaves a total repertoire of 222 elements was recorded. However, the estimated repertoire of individuals correlated closely with the number of processed handfuls of food analysed for each task, showing no sign of reaching asymptote. If massive samples of behaviour need to be analysed in detail even to count repertoire size, then the practical usefulness of this method is limited; but the problem seemed to stem

from relatively trivial variations in how a function was accomplished. This suggested an alternative approach of defining actions as different only if they had different effects on the plant material, regardless of the hand, fingers or precise action used. When such 'functionally equivalent' actions were used, much greater commonality between individuals was found, implying that estimates of repertoire were more reliable; in this case, 46 functionally distinct elements were found for thistle compared to 13 for nettle- and bedstraw-processing treated together.

Although repertoire-counting can evidently be used for broad comparisons, this method risks missing the most interesting aspects of task complexity. As an analogy, the English language has a very much larger lexicon of words than either French or Spanish, but few linguists would claim that English was therefore a more complex language. Similarly, a large repertoire of actions does not automatically equate to a complex task; the structural organization of behaviour is also critical. A rough and ready estimate of organizational complexity is given by the overall length of goal-directed sequences of action. Of course, an unstructured sequence of more or less randomly chosen actions may also be long, so it is necessary to focus only on strings of actions whose sequence is *repeated* on different occasions to achieve the same goal. Equally, as with repertoire-counting, care needs to be taken in delineating an action: to achieve a single effect, many unsuccessful attempts, or repeated identical actions with cumulative effect may be used. Here again, length does not equal complexity; one way to avoid inflated estimates is to split a process into *stages*, defined again by the effect upon the physical substrate.

This approach was also evaluated against the plant-processing tasks of mountain gorillas. For each task, individuals were found to have a small number of preferred techniques; among adults and juveniles, the number of techniques was found not to vary significantly with age (Byrne *et al.* 2001b). Qualitative differences among preferred techniques were themselves quite minor, and mainly a matter of which mirror form was preferred and slight variations associated with different plant material. Thus, for the local population of gorillas, a *modal technique* could be used to describe the skill common to all able-bodied individuals (Byrne & Byrne 1991, 1993; Byrne *et al.* 2001b). Flow charts give a convenient representation of modal techniques (see figure 1 for an example from the chimpanzee; Corp & Byrne 2002). While great ape feeding techniques show flexibility in response to variations in the problem presented by particular individual plants, the modal technique's organization is highly structured, so its length should give some indication of complexity.

In order to compare different feeding skills by calculating the length of the programme of actions needed to perform them, the start point was arbitrarily taken to be when the animal was in a position to reach the material (which might itself have required considerable effort and planning; see Russon 1998), and the end point was taken to be the ingestion of a mouthful of processed material ready to chew (although in many cases the individual then began work on processing the

Figure 1. Flow diagram showing the overall organization of behaviour and the apparent decision processes used in *Saba florida* fruit-processing (Corp & Byrne 2002). Actions are represented by boxes and decision processes by diamonds; when the underlying factor dictating a decision is unknown, this is denoted by a question mark. Square brackets enclose a series of options that each serves to achieve certain actions; choice between them is presumably a function of local stimulus conditions, rather than contributing to the overall complexity of the task organization.

next mouthful, and might continue for some time). Only feeding techniques signalled by regularly occurring, goal-directed activities were examined. Stages in the process were defined as composed of activity directed at a single effect on the world—in this case, on the plant material—in order to avoid inflating estimations by counting actions repeated for cumulative effect or owing to initial failures. When a stage occurred reliably when needed but was omitted whenever it was unnecessary, it was considered part of the modal process. Conversely, if several stages were repeated as a whole ‘subroutine’ more than once, in order to achieve a cumulatively greater effect, only a single sequence was considered. By these criteria,

mountain gorilla consumption of nettles *Laportea* and thistle *Carduus* were both found to be five-stage processes, whereas bedstraw *Galium* processing is a four-stage one (Byrne *et al.* 2001b; note that the precise way that the processed food was put into the mouth varied across these three cases, but ingestion was not counted as a separate stage, so the lengths may have been slightly underestimated). As can be seen from figure 1, chimpanzee consumption of *Saba* fruits is also a five-stage process by these criteria.

Comparable analysis has yet to be done for tool-based skills of the chimpanzee, but published accounts suggest similar or greater lengths in some cases (e.g. termite-fishing: pick stem, strip off leaves, bite end,

pick open termite hole, probe in, gently retract). In contrast, most monkey feeding is carried out by a one-stage process (see Panger *et al.* (2002) and O'Malley & Fedigan (2005) for some of the most elaborate processes yet described in monkeys).

While estimating the overall length of organized repeated processes is a more appropriate method of comparison than repertoire-counting, it is still by no means ideal. No account is taken of the potential complexity of hierarchical embedding of subroutines—if this indeed contributes to task complexity, which presumably would depend on the cognitive architecture of the animal, currently an unknown. No differentiation is made between stages which are more or less obligatory at a certain point in the process, or optionally omitted, or a matter of choice among several different options. And simply measuring length in stages does not take account of variations in the degree to which 'what to do next' at each stage is influenced by constraints in the local environment and the affordances of the animals' effector organs. At present, little research effort has gone into refining methods of estimating complexity, and these weaknesses may yet be circumvented. However, it may also be worth examining possible *correlates* of complexity—such as degree of individual or population-level laterality, or age of acquisition of techniques not limited by physical strength—to see whether these factors covary with sequence length.

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