PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2007) **362**, 603–620
doi:10.1098/rstb.2006.1998

The evolution of animal 'cultures' and social intelligence

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Decades-long field research has flowered into integrative studies that, together with experimental evidence for the requisite social learning capacities, have indicated a reliance on multiple traditions ('cultures') in a small number of species. It is increasingly evident that there is great variation in manifestations of social learning, tradition and culture among species, offering much scope for evolutionary analysis. Social learning has been identified in a range of vertebrate and invertebrate species, yet sustained traditions appear rarer, and the multiple traditions we call cultures are rarer still. Here, we examine relationships between this variation and both social intelligence—sophisticated information processing adapted to the social domain—and encephalization. First, we consider whether culture offers one particular confirmation of the social ('Machiavellian') intelligence hypothesis that certain kinds of social life (here, culture) select for intelligence: 'you need to be smart to sustain culture'. Phylogenetic comparisons, particularly focusing on our own study animals, the great apes, support this, but we also highlight some paradoxes in a broader taxonomic survey. Second, we use intraspecific variation to address the converse hypothesis that 'culture makes you smart', concluding that recent evidence for both chimpanzees and orang-utans support this proposition.

Keywords: social intelligence; social learning; tradition; culture; brain size

1. INTRODUCTION

The study of animal social intelligence has a pedigree of several decades (Whiten & Byrne 1988*a*, 1997, 2004), but has flourished in recent years through an exciting expansion of discoveries discussed throughout this issue. The topics of the present paper, spanning social learning, traditions and culture, have an arguably more ancient pedigree of over a century (Whiten & Ham 1992; Avital & Jablonka 2000 for reviews), yet recent years have likewise seen an enormous flowering of new knowledge in these areas. A diverse range of developments has been responsible for this, ranging from the coming-to-fruition of numerous long-term studies of specific species at different geographical locations, through the development of more refined experimental techniques, to advances in brain science and robotics. Up-to-date surveys of the resulting broad-ranging field can be found in Fragaszy & Perry (2003); *Evolutionary Anthropology* vol. 12, whole issues 2 & 3 (2003); Galef & Heyes (2004); Hurley & Chater (2005); Mesoudi *et al.* (2006*b*).

How does research in these domains relate to the topic of social intelligence? To a first approximation, the answer is that if social intelligence is taken to refer broadly to adaptive social information processing then the kinds of social learning implicated in the transmission of tradition and culture answer to this requirement. However, both of these terms, 'social intelligence' and 'social learning', cover an enormous range and diversity of phenomena. Accordingly, we begin by briefly examining the scope of each in turn and anticipating some possible links between them.

(a) *What is the scope of 'social intelligence'?*

If we can define intelligence then the rest is relatively easy, for social intelligence is essentially the intelligence applied to the social world. If, for example, we define intelligence as problem-solving ability, then social intelligence refers to a capacity to solve novel problems in one's social life. However, 'intelligence' is itself a term applied in highly varied ways in the psychology literature, from speed of associative learning to reasoning and innovation (Passingham 1981; Weiskrantz 1985). We suggest this history means that intelligence is nowadays best treated as a relatively broadly defined umbrella term that connotes relatively sophisticated forms of information processing, each of which requires more specific definition and more focussed investigation to generate real scientific progress. According to this logic, 'social intelligence' connotes relatively complex forms of information processing applied to the social world, a concept that thus has inherently fuzzy edges.

An influential reason for interest in animal social intelligence lies in the notion first explicitly elaborated by Nicholas Humphrey, and before him in more tentative forms by Michael Chance and Alison Jolly

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rstb.2006.1998 or via http://www.journals.royalsoc.ac.uk.

One contribution of 19 to a Dicussion Meeting Issue 'Social intelligence: from brain to culture'.

(Whiten & Byrne 1988*a*), that has become known as the 'Machiavellian Intelligence Hypothesis' (MIH; Byrne & Whiten 1988) or the 'Social Intellect Hypothesis' (SIH; Kummer *et al.* 1997). In broad terms, the MIH was originally developed to explain the special intelligence attributed to monkeys and apes (Humphrey 1976) as adaptations for dealing with the distinctive complexities of their social lives, such as volatile social alliances. The term 'Machiavellian' was used by Byrne & Whiten (1988) to capture the central concept of adaptive social manoeuvring within groups made up of companions subject to similar pressures to be socially smart, and the spiralling selection pressures this implies. With time, these central ideas have been applied to a variety of different species thought to display the relevant kinds of social complexity, as is evident in the present issue.

Although these hypotheses are frequently referred to as *the* SIH or *the* MIH, each can be expressed in terms that have significantly different implications, which are perhaps too often forgotten or unappreciated. Whiten & Byrne (1988*b*) distinguished three different, increasingly specific hypotheses:

(i) 'Intelligence is manifested in social life'. Historically, animal intelligence was investigated primarily in isolated individuals interacting with problems in the physical world, often in a laboratory setting. The mildest version of the MIH was simply that in reality, intelligence was to be observed operating also in certain animals' natural social worlds.

(ii) 'Complex society selects for enhanced intelligence'. This hypothesis proposes that there is something particularly challenging about the complexities of social life that select for greater intelligence. Here, 'intelligence' is regarded as a domain-general capacity (as in 'g'; Jensen 2000), contrasting with the third hypothesis.

(iii) 'Complex society shapes the forms intelligence takes'. This version of the hypothesis suggests that social interactions may have special properties that select not for generalized intelligence, but for particular forms of intelligence. Social intelligence might thus incorporate several dimensions or modules, each adapted to deal with a special social problem domain. An example well researched since 1988 is 'theory of mind' or 'mentalizing', the capacity to discriminate states of mind in other social beings, the underlying brain mechanisms for which are now being charted (Frith & Frith 2003).

Nowadays, Hypothesis 1 can be considered to be accepted, perhaps to the point of being thought obvious (with hindsight!). Hypotheses 2 and 3 remain more interesting and actively controversial. The primary way in which the MIH has been empirically tested is by examining interspecific relationships between encephalization and (i) social variables such as group size (predicted by the MIH) and (ii) ecological variables such as home range size (predicted by the competing hypothesis that foraging constitutes a more important selection pressure for intelligence) (Barton & Dunbar 1997; Dunbar & Shultz 2007). In such analyses, brain size is assumed to offer a summary index of cognitive capacity. Variations on this approach that examine particular parts of the brain, such as the neocortex ratio (neocortex relative to the remainder; Dunbar 1998) are often attempts to focus on the most 'intelligent' components of the brain, rather than dissect subcomponents implicated in more specific functions that might become more apt for testing Hypothesis 3. Such neuro-anatomical approaches are relevant to our studies of culture, because parallel techniques have been applied to test relationships between encephalization and social learning, reviewed in §2*a* below.

In the case of culture, hypotheses of type 3 will most obviously address the question of whether in species for which acquiring (and perhaps transmitting) culture becomes important or takes particular forms, there will be selection pressures honing the nature and functional significance of the relevant social learning processes. In addition, social structure may interact with these, generating complex mutual selection pressures between (i) the forms of social living, (ii) culture, and (iii) social learning mechanisms.

(b) *What is the scope of culture and how does it relate to social intelligence?*

Many authors equate culture and tradition, using the terms interchangeably. Others make distinctions between them of various kinds, usually requiring additional criteria to classify a phenomenon as cultural. Accordingly, there appears to be more agreement on what counts as a tradition than there is in the case of culture. A recent volume on 'The Biology of Traditions' defined tradition as 'a distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning' (Fragaszy & Perry 2003, p. xiii). This definition would probably be accepted by most researchers and we follow it here. Note that as indicated above, for many biologists, this definition of traditions will also be sufficient to define culture (Laland & Hoppitt 2003).

By contrast, authors for whom the existence of a tradition does not in itself warrant the ascription of culture typically require some additional characteristic(s) assumed to be associated with the complexity of traditions that constitute human culture. For example, Galef (1992), perhaps the most influential researcher in animal social learning, proposed that 'culture' be reserved for traditions transmitted by imitation or teaching, assumed to be high-level social learning processes that would imply homology with the human case. Others adopt different criteria such as that culture must accumulate complexity over time, as it has done so impressively in the human case; non-human species thus 'do not make the grade' (Levinson 2006, p. 10).[1]

Whether either imitation or teaching is crucial to support traditions, as Galef (1992) assumes, is an empirical issue not yet resolved (Whiten *et al.* 2003). Here, we focus on another distinction (although it may turn out to overlap much with Galef's in practice) that arises from the accumulating data on traditions in the animal kingdom, including the species we ourselves have studied (chimpanzees and orang-utans). This leads us to define culture as the possession of *multiple traditions*, *spanning different domains of behaviour*, such as foraging techniques and social customs (Whiten 2005). We think that a distinction between the existence of a tradition *per se*, and culture defined by a certain *complexity* in traditions, may prove an instructive one for evolutionary studies because (i) it makes reference to perhaps the most fundamental features of any two contrasting human cultures—that each is differentiated from the other by a multitude of different and varied types of tradition and (ii) as Galef himself argued, a higher criterion is set for culture than for tradition *per se*, giving us two levels in relation to which we can pursue detailed comparative analyses. We discuss this in more depth in §2*b* below.

Whether one treats tradition and culture as synonyms or not, an essential component in each is that transmission of behaviour between individuals occurs through social learning, which provides the obvious focus point for examining culture in relation to the general topic of social intelligence. At first sight, this aspect of culture might not be thought to fit well the perspective on social intelligence connoted by the 'Machiavellian' tag earlier promoted by one of us. However, in analysing the scope of Machiavellian Intelligence, both Whiten & Byrne (1988*b*) and Byrne & Whiten (1997) argued for the productivity of taking a wide, permissive perspective on the variety of socio-cognitive adaptations through which an individual may exploit the potential benefits of its social world, as well as deal with the hostile aspects of it. Whiten & Byrne (1988*b*) and Whiten (2000) accordingly recognized numerous potential facets to Machiavellian Intelligence: social knowledge; discovery techniques; social curiosity; social problem solving; innovation; flexibility; social expertise; social play; mind-reading; and self-awareness. Imitation and culture were also explicitly included. In the same volume, Hauser (1988, p. 326) suggested that 'social learning allows many individuals to 'become intelligent'. The title of Russon's (1997) chapter 'Exploiting the expertise of others' in *Machiavellian Intelligence II* indicates pithily how social learning relates to the larger concept. Jolly's (1966) and Humphrey's (1976) foundational papers also frequently addressed the topics of imitation and culture, and it is notable that the largest section in the most recent compilation of 'animal social complexity' research (de Waal & Tyack 2003) is headed 'cultural transmission'.

(c) *Exploring links between the evolution of culture and intelligence*[2]

Social learning, tradition and culture can each be investigated in relation to the three different versions of the MIH outlined in §1*a*. In relation to Hypothesis 2, we may accordingly ask whether there is evidence consistent with the hypothesis that a certain complexity of social life—in this case, the scale and diversity of traditions and/or culture—selects for intelligence. In §2*a* below, we first describe recent research that tackles this question by testing for correlations between encephalization and the prevalence of social learning in different animal taxa, echoing earlier tests of the MIH. In §2*b*, we extend this focus to review the distribution of cultural complexity among animals, finding evidence for this in only a small set of species, all of which are relatively highly encephalized.

In relation to Hypothesis 3, we can take a further step of asking whether there is evidence that complexity of culture selects for more sophisticated forms of social learning. We do this in §2*c*, focusing particularly on great apes, for which a suite of experimental studies has now been completed.

In addition to these hypotheses framed in relation to evolutionary selection processes, the phenomenon of culture raises the prospect of an ontogenetic version of the MIH, namely that being raised within a rich, accumulated culture can make an individual's ways of dealing with the world more intelligent: that 'culture can make you smart'. We are all familiar with this idea in human culture, for it is the basis of our educational systems. The idea becomes graphic when one compares a contemporary educated person with a person born with equivalent brain power just, say, 20 millennia in the past. Our present-day understanding of the world and the techniques available to us, for example, knowing the concept of the wheel and of horticulture (Mithen 2007), makes us truly smarter. In §3, we discuss evidence that in simpler ways, the same may be true in some non-human species. We attempt to complete the circle by discussing the evolutionary consequences of these ontogenetic effects on intelligence, suggesting that cultural species should more easily be able to reap the selective benefits of intelligence. This then links with the predictions of interspecific associations between culture and intelligence.

2. IS THE EVOLUTION OF SOCIAL INTELLIGENCE COUPLED WITH THE EVOLUTION OF TRADITIONS AND CULTURE?

(a) *Encephalization and social learning in primates*

The predictions of the MIH have mainly been tested against competing hypotheses by examining relationships between predictor variables such as social group size and indices of encephalization, with the outcomes increasingly supporting the MIH (Barton & Dunbar 1997; Dunbar 1998; but see Deaner *et al.* 2000). Early studies used social group size as a relatively crude proxy for social complexity (Dunbar 1995). More recent studies explored more refined measures. Thus, Kudo & Dunbar (2001) showed that the size of social cliques in a primate species was a good predictor of neocortex ratio (the ratio of the neocortex, generally implicated in higher mental processes, to the rest of the brain). Similarly, Byrne & Corp (2004) used the frequency of tactical deception (Whiten & Byrne 1988*c*), corrected for research effort, and found a strong relationship with neocortex ratio.

Reader & Laland (2002) have now extended this approach to include social learning and other related variables among primates, with interesting results. Reader and Laland scanned the primate literature, including approximately 1000 primate journal articles and other sources, extracting 445 reports of social learning, 533 reports of innovation and 607 reports of tool use, concerning 116 species of primate. They then

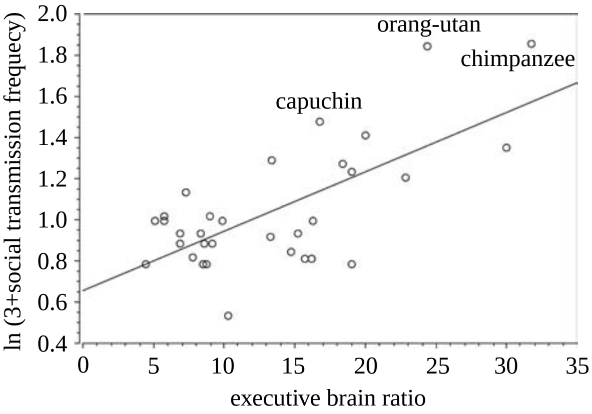

Figure 1. Social learning and encephalization in primates. Frequency of social learning in the survey of Reader & Laland (2002) is plotted against executive brain ratio (see text for further explanation). Labels added here refer to three species with complex cultures discussed extensively in the text.

examined relationships between the frequency of such reports, corrected for research effort, and three measures of encephalization, such as the executive brain ratio, which computes the ratio of the 'executive brain' (neocortex and striatum) to the brainstem. The use of several alternative brain indices, together with analysis through both correlation of raw data for all species, and more refined independent contrast methods that counter the risk of pseudo-replication arising from phylogenetic relatedness between species, added robustness to the conclusions of the study.

Of most relevance to the focus of the present paper, Reader and Laland found highly significant relationships between the prevalence of reports of social learning and executive brain ratio (figure 1). Similar correlations were also found for the frequency of innovation and tool use. In each case, the variance explained was remarkably high, with the highest $r^2=0.48$ for social learning, and $r^2=0.34$ and $r^2=0.40$ for innovation and tool use, respectively. Reader & Laland (2002, p. 4440) conclude these results 'suggest an alternative social intelligence hypothesis to those stressing the Machiavellian characteristics of mind-reading, manipulation, and deception', especially since they found no correlation between social group size (as mentioned above, a commonly used proxy for social complexity) and social learning frequency; instead, 'individuals capable of inventing new solutions to ecological challenges, or exploiting the discoveries and inventions of others, may have had a selective advantage over less able conspecifics, which generated selection for those brain regions that facilitate complex technical and social behaviour'. These conclusions thus do not support the proposition that social factors were more powerful than non-social in brain evolution; rather, they implicate a cognitive complex involving both innovation and social learning in the emergence of large brains among primates. This is an important finding in relation to the topic of this paper, for it is in the nature of culture to require both innovations and social learning processes, the latter being powerful enough to turn innovations into traditions. We will return to this in §3.

A recent Bayesian analysis of numerous studies of primate cognition found that species could be ranked on a single dimension of cognitive ability (Johnson *et al.* 2002). Deaner *et al.* (in press) found that this general cognitive ability was best predicted by absolute brain size, with the frequently used neocortex ratio a close second, indicating that these measures are reasonably good interspecific predictors of 'intelligence'. Together with Reader & Laland's (2002) finding that both innovation and social learning are correlated with an expansion of the executive brain in primates (and innovation also predicted neocortex ratio), these results suggest that innovation (as a form of intelligence), social learning (as a form of social intelligence) and encephalization evolved in concert. These are important results, although the indirect estimation of innovation and social learning tendencies, much of which relies on observers' judgements rather than experimental evidence, means that additional ways should be sought to further test these tentative conclusions.

Some remarkably convergent results have been reported for birds by Lefebvre *et al.* (2004). Using a very similar approach, they assembled an even larger database of 1796 records of avian innovation and found that the best predictor of innovation was the relative size of the hyperstriatum ventrale and neostriatum, structures described as analogous to the mammalian neocortex (Rehkamper & Zilles 1991; but see Avian Brain Nomenclature Consortium 2005; Emery & Clayton 2005 for revised neuroanatomical nomenclatures). In large-brained birds, these regions show the largest increases in size, like the neocortex in mammals (Rehkamper *et al.* 1991). Accordingly, in both mammals and birds, there is now evidence supporting a relationship between innovation and brain size.

Innovation, however, is but one half of what is required for traditions and culture: the other half is social learning. Lefebvre and colleagues did not investigate the relationship between social learning and encephalization, but the reason for this is itself of interest; the relevant data were relatively few. While there were 1796 observations of innovation, only 72 cases of social learning were recorded. This contrasts with the ratio of 558 cases of innovation and 451 of social learning in the primate study of Reader & Laland (2002). Lefebvre & Bouchard (2003, p. 110) conclude that 'what these relative numbers seem to suggest is that a feeding innovation does not as readily spread to others in birds at it does in primates', and that this appears to represent a paradox when contrasted with the fact that all 76 avian experimental studies they review successfully evoked social learning. We return to this puzzle in the concluding discussion.

(b) *The evolution of cultural complexity*

Reader & Laland's (2002) analysis did not explicitly examine traditions, but only social learning; nor did it examine the nature of the social learning. However, the picture of traditions and culture now emerging from decades of field research shows some interesting consistencies with their findings reviewed above.

Natural variations in behaviour in different communities of chimpanzees were increasingly recognized as

Table 1. Social traditions among capuchins (*C. capucinus*). Differential distribution of five social conventions across five study sites (after Perry *et al.* 2003*a*,*b*). Since finger game and hair game share the same distribution and share several behavioural characteristics, they may be regarded as a single tradition; thus, there are four traditions, differentiated by their distributions. Note that the profile for each community is unique.

	Lambas Barbadul, Abby group	Lambas Barbadul, Rambo group	Santa Rosa, Cerco	Santa Rosa, Nancite	Curú, Bette's group
hand-sniff: place another's hand or foot over own face and with eyes closed, inhale deeply and repeatedly over more than 1 min.	++	(+)	++	—	—
suck: suck lengthily on another's fingers, toes, ears or tails.	++	++	—	—	(+)
finger game: put finger(s) in mouth of another, who clamps down firmly, so lengthy effort required to withdraw finger(s).	++	—	—	—	—
hair game: monkey A bites tuft of hair from B, B extracts hair from A's mouth, A reciprocates, followed by more turn-taking.	++	—	—	—	—
toy game: turn-taking game extracting non-food objects (stick, leaf, bark, inedible fruit, etc.) from each other's mouths repeatedly.	++	—	—	—	++

likely traditions as field data accumulated, and began to be tabulated on the basis of published records (Goodall 1986; McGrew 1992; Boesch 1996; Boesch & Tomasello 1998). However, as Whiten *et al.* (1999) noted, reliance on published records generates an inevitably patchy and incomplete account. Instead, for the first time, Whiten and colleagues systematically pooled all the published and the unpublished information available from the most long-term study sites to identify as many as 39 traditions, defined as behaviour patterns common in at least one community, yet absent in at least one other, with no simple environmental explanation (such as that nut-cracking is absent because no suitable nuts are available). Identifying traditions in this way depends largely on integrating three sources of evidence: (i) exclusion of environmental or genetic explanations, which attribute the geographical variation to convergent individual learning or predispositions (clearest for many cases that involve differences between geographically close communities), (ii) relevant records of close, direct observation of adult expertise by novices, typically juveniles (Goodall 1973), and (iii) reliable background knowledge of the social learning propensities of chimpanzees, gained through controlled experiments (Tomasello & Call 1997).

Precisely the same approach was applied to orang-utans by van Schaik *et al.* (2003*a*), yielding a picture remarkably similar to that in the chimpanzee study in three important respects. First, traditions are numerous (19 clear cases plus a further 5 where ecological explanations could not be entirely excluded). Second, each community displays its own unique profile of traditions. Third, the traditions are of many different kinds, including tool use, foraging techniques, locomotory skills and social signals. Observational and experimental studies have also demonstrated a capacity for imitation and other forms of observational learning in orang-utans (Russon & Galdikas 1993; Stoinski & Whiten 2003; Whiten *et al.* 2004).

This threefold pattern of complexity in both chimpanzees and orang-utans goes beyond the mere existence of tradition and it is how we here mark off the more elaborate phenomenon of 'culture'. Looking towards humans, it is precisely this pattern of multiple and varied traditions that define each culture and differentiates it from others (e.g. Scottish versus English culture). Looking towards other non-human animals, this richness distinguishes what has been observed in great apes from most of the studies reporting animal traditions, that each typically cites only a single tradition. Lefebvre & Bouchard (2003), for example, tabulate 157 records of social learning in birds, in field and captivity, but none appear to correspond to multiple different behaviour patterns being transmitted. Similarly, birds with extensive geographical variation in song dialects do not stand out as having traditions in other domains (Catchpole & Slater 1995).

At the most pedantic level, our criterion for culture will mean that any species displaying at least two different traditions becomes eligible to be described as cultural. The more interesting implication is that as the total number of traditions rises and as the profile and diversity of traditions in each community increases, social inheritance becomes more all pervading, with potentially evolutionary effects on the sophistication of social learning, as well as other characteristics like life-history variables. On this perspective, it is likely that the complexity of culture will be manifested in many different evolutionary grades, rather than in an all-or-none fashion.

Apes are not the only non-human animals to meet our criteria, as several recent reports attest. Perhaps the most thorough and persuasive evidence concerns capuchin monkeys (*Cebus* spp.). Perry *et al.* (2003*a*,*b*) have described several social conventions that differ between populations of white-faced capuchins (*Cebus capucinus*; table 1) and meet our cultural criteria. Ascription of social transmission in this case is particularly strong, because in the case of such purely

Table 2. Examples of putative foraging traditions among capuchins (*C. capucinus*). Eight examples of differential distribution of foraging patterns across three study sites, drawn from the larger chart of Panger *et al.* (2002). Two examples for each of 'pound' and 'rub' are differentiated only by the way the techniques are applied to specific targets: the patterns of pound and rub are universal, shown at all study sites. (C, customary (performed by most individuals); H, habitual (performed repeatedly by several individuals, consistent with social diffusion); —, absent without ecological explanation.)

	Lomas Barbudal	Palo Verde	Santa Rosa
army ant following: several monkeys follow foraging ant column and catch prey flushed by ants.	—	—	H
fulcrum use: using force on an object against a substrate acting as fulcrum, as in breaking fruit to obtain beetles inside.	—	H	H
leaf wrap: wrap object in leaf then rub leaf against substrate, protecting hands—applied to *Autmeris* spp. caterpillars	H	—	H
tap: tap against object using fingertips—probably checking fruit ripeness, presence of insects in wood—applied to *Stemandia*.	—	—	C
pound: hit object against fixed substrate—applied to *Randia* fruits.	H	H	—
pound: hit object against fixed substrate—applied to *Cecropia* fruits.	—	—	C
rub: slide an object against a surface—applied to *Tabebuia*.	C	H	—
rub: slide an object against a surface—applied to *Pithecellobium*.	—	—	C

Table 3. Examples of traditions among orang-utans. Six examples illustrate the differential distributions that define different traditions; the diversity of types of behaviour patterns involved (cf. universal patterns of pound and rub in table 2); and the unique profiles that define local cultures. These examples are drawn from the full list of 19–24 (van Schaik *et al.* 2003*a*). (C, customary (performed by most individuals); H, habitual (performed repeatedly by several individuals, consistent with social diffusion); —, absent without ecological explanation; r, rare; e, absent for ecological reasons.)

	Gunung Palung (Borneo)	Tanjung Puting (Borneo)	Kutai (Borneo)	Lower Kinaba-tangan (Borneo)	Leuser Ketambe (Sumatra)	Leuser Suaq Balimbing (Sumatra)
snag-riding: ride on pushed-over snag as it falls, then grab onto vegetation before it crashes on ground.	—	C	—	—	—	—
kiss-squeak with leaves: using leaves on mouth to amplify sound, then drop leaf.	C	—	H	—	—	—
sun cover: building cover on nest during bright sunshine (rather than rain).	—	?	C	C	H	—
leaf gloves: using leaf gloves to handle spiny leaves or spiny branch, or as seat cushions in trees with spines.	—	r	—	—	H	e
tree-hole tool use: using tool to poke into tree holes to obtain social insects or their products.	—	—	—	—	—	C
branch scoop: drinking water from deep tree hole using leafy branch (water dripping from leaves).	—	—	—	—	—	H

social conventions, it is difficult to envisage alternative ecological explanations. Moreover, the observed rise and later attenuation of these behaviour patterns over a period of years argues against their being transmitted genetically. However, this ephemeral character appears to distinguish them from most cultural variants described for great apes, many of which have been recorded for decades. Foraging behaviour also differs between sites in ways that suggest social transmission (Panger *et al.* 2002); examples are shown in table 2. The complete set of published comparisons includes over 20 such variations. However, this tally cannot be directly used to compare cultural complexity with the apes, because the capuchin records concern just six main techniques (the level at which the 39 chimpanzees records are described, for example; table 3 for comparison), differentiated at the study sites in terms of how they are applied to specific foodstuffs (e.g. 'Rub *Sterculia* fruit' is habitual at Lomas Barbadul (LB) yet absent at Palo Verde (PV), whereas 'Rub *Sterculia* husks' is habitual only at PV; and 'Rub *Acacia* thorns' is habitual only at Santa Rosa (SR)). Finally, Rose *et al.* (2003) offer additional data indicating traditions concerning interactions with other species. For example, LB monkeys catch and kill squirrels with a bite to the neck, whereas SR monkeys start to eat them before killing.

Although it is not appropriate to attempt direct numerical comparisons between the complexity of ape and capuchin cultures,[3] capuchins do fit our criteria for culture, assuming these comparisons are confirmed by detailed future observations. The reason for this convergence between capuchins and great apes is not entirely clear, for although capuchins have unusually large brains for their body size, they neither have large brains in absolute terms nor high neocortex ratios (Rumbaugh *et al.* 1996; Deaner *et al.* in press). Perhaps the greatest convergences with great apes are their slow development and remarkably high social tolerance, creating extensive opportunities for social learning.

The other group of mammals that has been claimed to exhibit cultural complexity is cetaceans (Rendell & Whitehead 2001), although it is generally acknowledged that constraints on observation limit the inferences that can reliably be made so far. Dolphins present perhaps the most comprehensive information to date, although to our knowledge, systematic collaborative studies like those reported above for primates remain to be completed. Nevertheless, Mann & Sargeant (2003) note that evidence of population-specific foraging techniques includes sponge-carrying, thought to be used to ferret fish from the sea bed (Smolker *et al.* 1997; Krützen *et al.* 2005), tail-whacking the surface to scare up fish (Connor *et al.* 2000), belly up chasing of fish at the surface (Mann & Smuts 1999) and several others. In addition, Mann & Sargeant (2003) identify correlation between mothers and daughters for many of 11 different foraging techniques, as well as in the overall size of their repertoire, within a single population of dolphins. The authors conclude that adding to existing evidence of acoustic traditions in cetaceans (Janik & Slater 1997, 2000), 'our data suggest that elaborate motor skills can also be socially learned and maintained across generations' (p. 262). They do not discuss the possibility of a role for genetic inheritance in the mother–calf concordances in behaviour, presumably seeing this as implausible given the range and diversity of techniques involved (but see Krützen *et al.* 2005). If the putative traditions of dolphins and other cetaceans are indeed socially transmitted, then once again cultural complexity is manifest, and here we are dealing with species with the highest encephalization among non-human animals. Mammals meeting the criteria for complex culture are thus, so far, those that can be described as relatively highly encephalized on one or more indices.

Among birds, the most likely candidate for multiple tradition culture is the New Caledonian crow (*Corvus moneduloides*), which uses at least two different tools (twigs, and strips cut from the edges of *Pandanus* leaves, the barbed edges of which make the tool particularly effective) to extract invertebrates like caterpillars from crevices (Hunt 1996, 2000). On various parts of New Caledonia, crows cut leaves to different designs ranging from a simple step shape to ones with several steps, the latter providing a thicker 'handle' at one end and a tapering tip at the other, both apparently making the tool more effective. These variations form a graded series with a distribution across New Caledonia that is consistent with cumulative evolution of step-complexity as the habit diffused through the population (Hunt & Gray 2003). This raises the prospect not only of multiple traditions, consistent with our notion of culture, but of cumulative cultural evolution, for which there is only the weakest evidence in primates other than humans (Whiten *et al.* 2003). However, some doubt over the role of social learning has arisen because naive captive crows of this species have been shown to spontaneously cut and use *Pandanus* tools on first contact with leaves of the plant (Kenward *et al.* 2005), echoing the finding that woodpecker finches, the other bird species to use stick tools, do not depend on social learning in acquiring tool use (Tebbich *et al.* 2001). This contrasts with experimental evidence for social learning of tool use in captive apes. In a recent study, Whiten *et al.* (2005) trained one individual from each of two groups of chimpanzees to use a tool in just one of two alternative ways to free trapped food items, and showed that each technique spread preferentially in the group it was seeded in, creating traditions. Similar experimental evidence now extends to non-tool actions (Horner *et al.* 2006; Bonnie *et al.* 2007). Until similar studies are done with corvids, the findings of Kenward *et al.* suggest caution is needed in concluding that the two kinds of tool use shown by these animals represent multiple traditions. Since crows in the experiment did not make stepped tools, it remains a possibility that a predisposition exists to strip leaf tools, but that social learning is required to refine this into one of the forms of stepped tool making. Further experiments are needed to test this.

We end this section with a note of caution. In most cases, the evidence for animal cultures in the wild is still incomplete, in that the major alternatives, individual learning due to ecological conditions or genetic predispositions, have not been refuted to the satisfaction of all (e.g. Galef 2003; Laland & Janik 2006). Thus, the conclusion that these taxa possess rich cultures is preliminary; it has become parsimonious for the great apes and capuchins, but remains controversial for other taxa. Further studies are needed to confirm these emerging patterns.

(c) *Does culture call for (social) intelligence?*

A 'cultural' version of the MIH would translate as: 'cultural complexity selects for intelligence', where cultural complexity refers to the scale, diversity of function and cognitive sophistication of the traditions concerned. This would correspond to MIH type 2 (p. 2), referring to general, and generalizable intelligence. Alternatively, one might predict, as in MIH type 3 (p. 2), that intelligence would in this case be shaped to particular forms, presumably involving social learning, the aspect of cognition most obviously necessary for a cultural animal.

Social learning of the simplest kinds has increasingly been identified among vertebrates and also invertebrates (Coolen *et al.* 2006; Worden & Papaj 2005). However, such social learning can serve a variety of purposes such as gaining useful information about local foraging hotspots, and other eavesdropping functions useful in the very short term, yet not necessarily the basis for traditions (Danchin *et al.* 2004). Perhaps the social learning associated with culturally complex species is more sophisticated? We address this question further below.

However, culture also requires innovation. This complicates the picture, predicting that culturally complex species will also be stronger innovators; and this in turn might seem to make it difficult in practice to differentiate enhanced general intelligence under MIH 2 (which might be applied to both social and non-social worlds) from the existence of cognitive capacities specialized for social learning and intelligent innovation, respectively, as predicted by MIH 3.

One reason to think the latter is at least plausible comes from research on autism in humans. Autistic spectrum disorders have become well known for providing some of the clearest evidence for modularity in social intelligence, for individuals with Asperger's syndrome in particular are often high in general intelligence, yet show deficits and delays in their mentalizing, or theory of mind (Frith & Frith 1999). More recently, it has become appreciated that autism is also associated with difficulties in imitation in childhood (Whiten 1996; Williams *et al.* 2004). Thus, there can indeed be independence between the cognitive machinery for this form of social learning and non-social aspects of intelligence in a primate.

Turning to comparative studies of primates, data appear to fit the prediction of MIH 3 insofar as the apes with the most complex cultures show evidence of imitation, whereas such evidence has been remarkably lacking for monkeys (Visalberghi & Fragaszy 1990, 2002; but see Voelkl & Huber 2000). However, widening the perspective, a series of carefully controlled 'two-action' studies has recently demonstrated imitation in birds, including pigeons, quails, starlings and budgerigars (Zentall 2004), which are not relatively encephalized and for which culture has not been claimed in the sense we define it. In their comprehensive avian review, Lefebvre & Bouchard (2003) noted the paradox that their database recorded few episodes of spontaneous social learning in birds when compared with those available for primates, whereas experimental laboratory studies typically returned positive evidence of social learning more often in birds than in monkeys and other mammals. We discuss these puzzles in §4 of this paper. In the present section, we focus instead on chimpanzees and orang-utans, where the scale of cultural complexity still appears considerably greater than in any other non-human species, and we ask whether there is evidence that their social learning displays the greater sophistication this predicts. A more comprehensive analysis than can be offered here is in Whiten *et al.* (2004).

(i) *Dimensions of encoding*

Two-action studies with birds have tended to demonstrate imitation that is close to two-dimensional (e.g. push manipulandum to left versus right; Klein & Zentall 2003; push bung down versus pull it out: Heyes & Saggerson 2002) or binary (depress treadle with beak versus foot; Zentall *et al.* 1996). By contrast, in studies in which chimpanzees and orang-utans have been trained to 'Do-as-I-do' (Custance *et al.* 1995; Call 2001), an elaborate three-dimensional mapping has been confirmed that extends to matching acts directed at many different points of the body, and coordinating manual and other configurations at detailed levels. Examples in the category 'asymmetric use of hands' are 'clap one hand on back of other' versus 'clap two digits on other palm' and 'grab thumb of other hand'. This suggests that apes may be able to encode complex dimensions of action that bear some correspondence to the enormous diversity of actions possible with a pair of primate hands. Unfortunately, comparative studies are constrained because other species have failed to grasp the concept of 'Do-as-I-do' (§2*c*(iv) below).

(ii) *Rationality in copying*

Another way to address the issue of intelligence in social learning is to ask whether when apes ape, they do so blindly or selectively. Horner & Whiten (2005) presented young chimpanzees with either of two boxes with top and front holes, protected by various defences. A familiar human model tackled each box in the same way, first ramming a stick tool into the top hole several times, then withdrawing it and inserting it into the front hole to extract a food reward. Although the food was hidden in a central tunnel in both boxes, one box was otherwise transparent, so that the initial ramming action could be seen to be ineffectual, beating on a false ceiling, which was not apparent with the alternative, opaque box. Chimpanzees tended to repeat all actions in the latter case, but to omit probing in the top hole after witnessing the model do this ineffectually with the transparent version, indicating their copying was rationally selective. In this experiment, it was in fact young children who were the indiscriminate copiers, probing in the top hole with either box. This intriguing result implies that rationality may not be crucial for significant cultural learning to occur. However, this is not necessarily inconsistent with the view that rationality has been important in making human culture as a whole as sophisticated as it is.

(iii) *Copying sequential structure*

Whiten (1998) presented chimpanzees with a human model performing a series of acts required to open an 'artificial fruit' in different, sequential orders. By the third demonstration and attempt, subjects almost perfectly matched the sequence witnessed. The study of Horner & Whiten (2005) described above offers complementary evidence that chimpanzees do not merely 'replay' the chain of events witnessed, but can instead parse it (Byrne 2000) before assembling their own version, because in the opaque box condition, they repeated both acts in the correct order (probe top, then bottom) whereas in the transparent condition, they tended to perform only the second of these. These studies suggest that chimpanzees may have at least some capacity to grasp the higher-level structure of complex actions and copy them, going some way towards the more elaborate concept of hierarchically sensitive 'program-level imitation' hypothesized by Byrne & Russon (1998). Nguyen *et al.* (2005) have since provided evidence that pigeons will imitate a chain of two events, such as stepping on a treadle and then pushing a screen, but did not test whether they would copy alternative sequential organizations of the elements involved (treadle–screen versus screen–treadle).

(iv) *Recognizing the imitative process*

The fact that chimpanzees and orang-utans have been able to learn the 'do-as-I-do' routine implies that they can grasp, or learn, a concept of what counts as imitation. Interestingly, attempts to train this in monkeys have failed (capuchins, Fragaszy *et al.* unpublished, cited in Visalberghi & Fragaszy 2002; macaques, Mitchell & Anderson 1993). Dolphins have grasped the concept (Herman 2002), raising the prospect that there is a link with the ability to recognize oneself in a mirror, which is also known only for the great apes (including humans of course; Tomasello & Call 1997) and dolphins (Reiss & Marino 2001), an otherwise remarkable coincidence. Just what the significance of this is for everyday social learning remains something of a mystery but it does appear to put the social cognition underlying ape imitation onto some qualitatively higher plane.

The scope of culture in great apes may also be predicted to have effects on other related aspects of social cognition. One is conformity to cultural norms. The chimpanzees in the Whiten (1998) study described above discovered some alternative sequences that worked, but nevertheless converged on the sequence used by the model, suggested an element of conformity akin to that identified in humans (Asch 1956), but has remained unconfirmed in the literature. More recently, in a two-action diffusion study, some chimpanzees likewise discovered for themselves the alternative technique seeded in a different group but rare in their own, yet later re-converged on the norm for their group, demonstrating conformity in the face of discovering a functional alternative themselves (Whiten *et al.* 2005). In one sense, this is the opposite of intelligent—it could even be re-described as 'mindlessly following the herd'. However, it is a marked characteristic of human cultural behaviour and requires a capacity to recognize the local norm and react to it. Yet, conformity of the basic 'follow the majority' kind has been demonstrated in a variety of species including fish (Day *et al.* 2001). What may be distinctive about the chimpanzee and human cases is that conformity overrides the discovery of valid alternative means. It is therefore better thought of as a particularly strong motivation to copy others rather than use one's own knowledge. This may become the more adaptive when cultural transmission is pervasive in reasonably stable environments (Henrich & Boyd 1998).

3. DOES CULTURE MAKE YOU SMART?

The phenotypic expression of all traits depends on the interplay between genetic factors and the effects of environmental conditions, both internal and external to the organism, during development (West-Eberhard 2003). The extent to which environmental influences can affect the adult phenotype varies across traits and species, and at least some of this variability may reflect adaptations. Developmental plasticity is greater for many behavioural features than for morphological ones, especially for behaviours that rely on cognitive processes emanating in the cortical brain regions (Rosa & Tweedale 2005). Thus, although a species' intelligence is often considered an innate given, we should rather expect it to be affected by the interaction between innate components and environmental inputs during development. This expectation is, of course, amply met in humans, where numerous studies have examined the interaction between genetic endowment and developmental inputs in determining intelligence (Jensen 2000). Environmental shaping of intelligence might be expected more generally in primates owing to their relatively large adult brains (Passingham 1981), very slow development (Case 1978) and extensive postnatal brain growth and differentiation, the extent of which is an excellent predictor of the duration of immaturity (Barrickman *et al.* in review), and therefore of the time available for learning.

In species where immature individuals are in close association with parents, caretakers or other tolerant adults, social learning may be additionally facilitated. Social learning can improve the signal:noise ratio in available information relative to independent individual exploration, and the frequency of opportunities for social learning may therefore enhance adult cognitive performance more than an equal number of opportunities for individual exploration and learning. Such a positive impact of social learning on realized intelligence might occur merely through selective attention to those stimuli and contexts where the acquisition of valuable skills is most likely. If more specialized social learning mechanisms are available, such as those discussed in §2*c* above, then cognitively richer, more rarely invented innovations may be more reliably acquired by maturing individuals and their fitness enhanced accordingly.

To van Schaik (2006), these *a priori* arguments suggest not only a dependence of adult cognitive abilities on the quality and quantity of environmental inputs during development, in primates and probably other animals with long development periods, but more importantly, a special role for social learning in this process. To test these conjectures, we can turn first to experiments that artificially reduce or increase environmental inputs during primate development. Social deprivation is well known to lead to major cognitive deficits in rhesus monkeys, as demonstrated by numerous classical studies (e.g. Sackett *et al.* 1999). The opposite of deprivation, enrichment, may produce increases in cognitive performance. Indeed, in captivity, where animals have access to enriched material conditions and no need for frequent vigilance, a far greater number of primate species is capable of using and even making tools, in the absence of obvious conditioning, than is documented from the wild (van Schaik *et al.* 1999). The enculturation effect, observed when great ape infants are raised like human children, similarly suggests that increases in socially guided exploration opportunities bring about enhanced cognitive performance (Gardner & Gardner 1989; Tomasello & Call 2004). Perhaps the most striking effect of enculturation has been in producing unusually elaborate comprehension of human language in great apes that do not use such symbolic signalling in the wild (Savage-Rumbaugh & Levin 1994). Thus, the intelligence of adult primates is clearly impacted by experimentally induced variation in environmental conditions during development, some of them socially mediated.

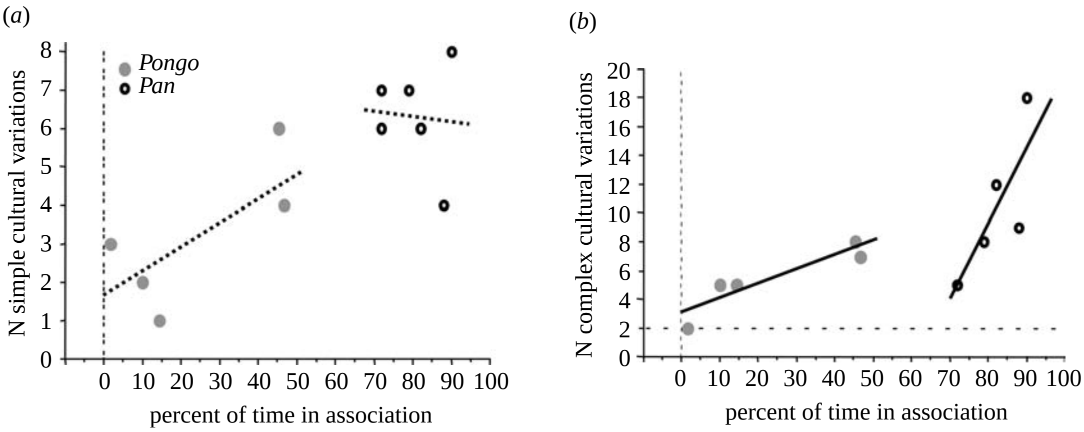

Figure 2. Relationship between association time and number of cultural variants across populations of orang-utans or chimpanzees, for (*a*) cognitively simple and (*b*) cognitively complex variants. For (*a*), analysis of covariance reveals no significant effects of association or species, nor of their interaction; for (*b*) all these effects are significant (association, $p=0.003$; species, $p=0.01$; interaction, $p=0.02$). Data on cultural variants are from Whiten *et al.* (1999) for chimpanzees, and van Schaik *et al.* (2003*a*) for orang-utans; see text and endnote 4 for assignment of cognitive complexity of variants. Animals were 'in association' when they had one or more independent conspecifics at less than 40 or 50 m (variable between studies); data from Boesch (1996) for chimpanzees and van Schaik *et al.* (2003*a*) for orang-utans.

Is there enough variation in nature to expect similar effects of developmentally differentiated social inputs on adult cognitive performance? The fact that great ape populations vary widely in the degree to which animals spend time together in tolerant proximity could affect the frequency of opportunities for social learning in this way, and thus perhaps later cognitive performance. East African chimpanzee females may spend over half of their time alone (Wrangham *et al.* 1996), especially when they have dependent infants, whereas West African females tend to be gregarious, even if they have infants (Boesch & Boesch-Achermann 2000). Among orang-utans, on average less gregarious than chimpanzees, Bornean females are much less gregarious than Sumatran females (van Schaik *et al.* 1999). Only Sumatran orang-utans share food outside the mother–infant context, and among Sumatrans this food sharing is most pronounced at Suaq Balimbing, where close proximity (less than 2 m) is by far the most common (van Schaik 2004). Similarly, the more gregarious West-African chimpanzees also show greater social tolerance, with food sharing being a more orderly process, under control of the original owner of the food (Boesch & Boesch-Achermann 2000), whereas in the less gregarious East-African chimpanzees, food sharing appears better characterized as sharing under pressure (Gilby 2006).

The field data for both chimpanzees and orang-utans show that inter-population variation in tolerant proximity is positively correlated with the number of cultural variants classed as cognitively complex in each population, whereas the relationship is not significant for variants that appear more cognitively simple (figure 2).[4] Cultural variants, by definition, are innovations that have become common in a population through social learning. The relationship in figure 2 suggests that cognitively complex cultural variants are more likely to be invented or maintained in populations with more opportunities for close-range social interactions. Figure 2 also suggests that chimpanzees have greater repertoire sizes than orang-utans. This species difference is consistent with the same principles, because overall, chimpanzees are more gregarious than orang-utans.[5]

The relationships illustrated in figure 2 are correlations and must therefore be interpreted with appropriate care. However, it is unlikely that variation in cultural repertoires causes differences in gregariousness, because gregariousness does not depend on particular contexts in which especially valuable cultural variants are performed. Indeed, gregariousness in orang-utans is better explained by local ecological productivity (van Schaik 2004). Hence, we infer that the causal arrow is most likely to run from tolerant gregariousness to the size of the cultural repertoire.

Several alternative mechanisms might explain this. One possibility is that animals in more gregarious populations have higher developmentally enhanced general intelligence and are thus more likely to invent cognitively complex innovations. An alternative hypothesis is that these animals encounter more innovations, including those that can form the point of origin for more complex versions. Data currently available are insufficient to properly distinguish these propositions. In either case, however, the outcome is that individuals in populations with more tolerant gregariousness end up performing more cognitively complex behaviours, and can therefore be considered more intelligent in this respect as adults.

What happens across populations is also to some extent seen within populations. Among the orang-utans at Suaq Balimbing, for instance, tree-hole tool use, while customary (van Schaik *et al.* 2003*a*), does show remarkable variation in its rate (van Schaik *et al.* 2003*b*). The females can be divided into clusters, based on range use and association (Singleton & van Schaik 2002). The northern females at the site are far less gregarious than the central and southern females—a difference that is stable over time and also includes maturing females, who tend to settle in or near their natal range. However, their home ranges show large overlap, and in the overlap zone they are equally likely to forage for insects and hence have equal opportunity to engage in tree-hole tool use, yet the northern females

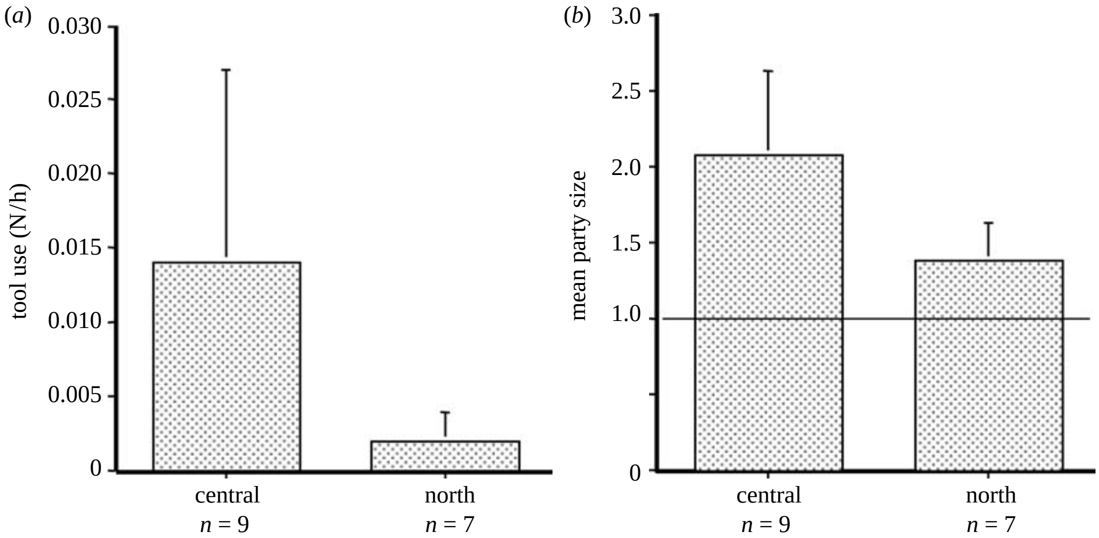

Figure 3. The propensity to use tree-hole tools in two clusters of (sub)adult orang-utan females at Suaq Balimbing that vary in mean party size (including only independent individuals in association with focal females; hence, minimum party size is 1). Numbers in parentheses indicate the number of females; vertical bars are standard deviations. Results of *t*-tests for tool use rate: $p<0.05$; for party size: $p<0.01$. Party size differences among females remained constant over time, including following maturation. Data from van Schaik *et al.* (2003*b*).

do so far less (figure 3). Since they occasionally do so, we assume that they know in principle how to solve the task if they encounter it. This suggests that they have more difficulty recognizing when the opportunity presents itself. The difference, then, is probably primarily one of experience in recognizing tree holes that are good for tool use. This experience is probably built up during the formative years, and may depend dramatically on the frequency of opportunities to engage in the task from start to finish during this period. The central and southern females are far more gregarious, therefore much more likely to accompany experienced foragers, and to develop a sharp search image for opportunities for tool-supported extractive use of tree holes.

Overall, then, there is circumstantial evidence for the impact of developmental inputs on adult cognitive performance in wild great apes. There is no evidence for intraspecific variation in other primates as yet, but the above-mentioned deprivation experiments suggest that we should expect similar variation in monkeys, and perhaps other organisms as well. Variation in the frequency of opportunities for close-range social learning may also partially determine differences in cognitive performance across species. This may be particularly relevant to understanding the prevalence of traditions among capuchins, for as noted above, these monkeys develop slowly and form unusually tolerant societies.

4. CONCLUDING DISCUSSION

The emerging picture of social learning, traditions and culture appears to have the form of a pyramid, the base of which represents the occurrence of social information transfer of many different kinds in many taxa of the animal kingdom (figure 4; see also van Schaik *et al.* 1999; van Schaik 2004; for related evolutionary models). Social learning, at least in its simpler forms, is well established in mammals, birds and fish (Laland & Hoppitt 2003) and recent reports extend to invertebrates (Worden & Papaj 2005). Much of this learning exploits public information that is functional in the shorter term, such as learning about temporarily productive foraging patches or avoiding the current location of a predator (Danchin *et al.* 2004), rather than the consistent habits we call traditions. Sustained traditions thus constitute the second, smaller layer of the pyramid, built upon the existence of social information transfer. How much social learning eventuates in traditions and how much serves

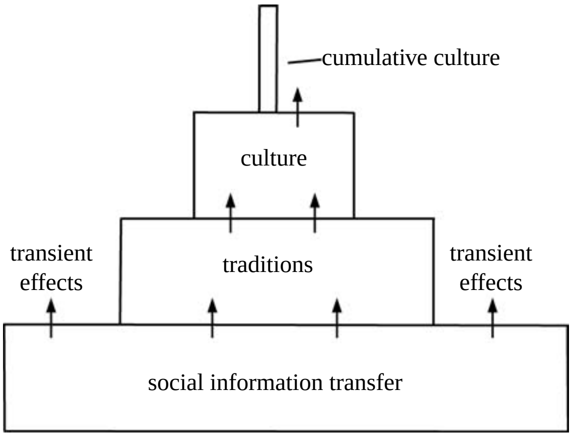

Figure 4. Culture pyramid. Social information transfer (foundation layer) is widespread in vertebrates and occurs also in invertebrates (see text for references). However, only a subset of such transfer eventuates in sustained traditions (layer two), because effects of social learning are often transitory only (e.g. using public information to judge profitable foraging patches). The occurrence of traditions may also be more restricted taxonomically than use of social information *per se*. More rarely still, cultures exist that are defined by the existence in the same species of multiple traditions forming unique local complexes (layer three). Cumulative culture (layer 4) occurs when more complex traditions arise by elaboration on earlier ones, generating the richness of human cultures yet minimally evidenced in other species. Relative sizes of each layer are notional. Arrows indicate the reliance of each layer on pre-existing lower layers.

shorter-term functions, whether in terms of learning events, or representation in different animal taxa, is at present difficult to estimate. The answer will probably be different for different levels of social learning and in any case presents formidable problems of appropriate measurement in practice.

The existence of a tradition does not yet constitute culture as we define it. It is the third layer of the pyramid that thus represents the occurrence of the multiple and diverse sets of traditions we call cultures. The evidence for such cultures that we have reviewed in this paper indicates that in contrast to the occurrence of traditions in a wide range of vertebrates including fish, only an as-yet small set of relative highly encephalized, socially living mammalian taxa show significant cultural complexity. The fourth level of the pyramid represents cumulative cultural evolution, in which more sophisticated traditions are progressively built through elaboration on earlier ones. It is this process that has evidently been responsible for the current complexity of human culture, from our languages to our diverse and burgeoning technologies. Evidence for cumulative culture in non-human species is minimal at best (Whiten *et al.* 2003; but see McGrew 2005; Byrne 2007), which appears to explain the major gulf between the content of human versus non-human culture (Boyd & Richerson 1996; Tomasello 1999).

Taken together, the inter- and intraspecific correlations we identified between cultural complexity, social learning capacities, social learning opportunities and encephalization suggest an evolutionarily spiralling process in which social learning may engender traditions, the emergence of multiple traditions selects for enhanced social learning, multiple traditions generate smarter individuals, smarter individuals innovate and learn better, and there is associated selection for encephalization; moreover, positive feedback is expected between many of these effects. Other characteristics may additionally be associated with this 'adaptive complex' that we have insufficient space to discuss in matching detail, prime candidates being life-history variables such as the length of the juvenile period of dependency on parents (van Schaik *et al.* 1999). For example, there is evidence in birds that relative brain size is well predicted by how long young birds stay with their parents after fledging, a period of potential apprenticeship (Iwaniuk & Nelson 2003). It may be that the encephalization involved here reflects not only neural tissue devoted to social learning mechanisms, but also the storage needs for all that is acquired and remembered in this apprenticeship. In apes, this cultural knowledge-base—of 'know-how' and 'knowing-that' must be very demanding of neural storage provision; more particularly, the demands of storing all that is learned culturally by humans (language, technology and the rest) may explain more of our extraordinary encephalization than has been appreciated.

The central links we have proposed here between complex culture and intelligence constitute a 'Cultural Intelligence Hypothesis' (CIH) that can be seen as complementing the MIH. A CIH can be regarded as a particular instance of the 'behavioural drive' and 'cultural drive' hypotheses described by Wyles *et al.* (1983) and Wilson (1985), respectively, which proposed that a combination of innovation and social learning allowed some taxa to more effectively invade new niche space through behavioural means, in turn driving biological evolution at higher rates. Wilson and his colleagues argued that these effects are notable in mammals and birds particularly, their hypothesis being supported by an almost perfect correlation ($r=0.97$) between relative brain size and rate of anatomical evolution across major groups of reptiles, amphibians, mammals and birds (the arbitrariness of some of the specific taxonomic contrasts used urges caution in taking this correlation at face value; but see Sol *et al.* (2005) for avian analyses consistent with Wilson *et al.*'s hypothesis).

The hypothesis of Wyles *et al.* has interesting precursors, not cited by these authors, such as that now referred to as the Baldwin effect (see Bateson 1988; Baldwin 1902), which posits that behavioural innovation may permit certain species to invade new niches, thus modifying selection pressures that in turn cause corresponding, genetically based changes. Other theoretical affinities that merit exploration are with more recent hypotheses described as cultural niche construction (Laland *et al.* 2000), in which the traditions that animals themselves create become part of the selective landscape affecting other characteristics, such as encephalization and life-history strategy. In similar vein, Tomasello (1999) has offered a detailed case for the evolutionary shaping of human cognitive capabilities by the special characteristics of culture that arose in our species.

Of particular interest, for the present issue, is that the CIH joins a growing family of selection hypotheses whose distinctive feature is positive feedback, creating the potential for spiralling, or runaway, evolution (Bateson 2004). Thus, as in the MIH itself, as well as in sexual selection and behavioural drive, evolutionary change is predicted to be racked up without any necessary pressure from the external environment, but instead through spiralling interactions between conspecifics. In the case of the MIH, CIH and behavioural drive hypotheses, 'socially intelligent conspecifics' are key. The central idea in all of these proposals is that whatever the cause of an initial rise in social intelligence, the fact that this is manifested in social interactions means that an increase in intelligence in any one individual selects for increases in others, and so on in spiralling, positive-feedback fashion. As in the case of sexual selection, this is potentially a runaway process. Of course some additional factor must eventually apply a brake, where the costs (for example, of manufacturing and maintaining expensive brain tissue) outweigh benefits in the current ecological niche. Conversely, additional factors must be identified to explain the release of such a brake in a particular case, as happened in the exceptional escalation in encephalization, social intelligence and cultural complexity that occurred in hominin evolution (Whiten 1999, 2006; and see Mithen 2007; Sterelny 2007).

If the CIH is suggested by what we know of chimpanzees and orang-utans, are its predictions supported by data from the other taxa we discussed? The evidence from cetaceans is supportive, insofar as there is evidence for multiple and diverse traditions, particularly in some specific cases including dolphins and killer whales, and these species are among the most highly encephalized mammals. Dolphins have demonstrated perhaps the most impressive imitative capacity of any non-human animals, great apes included, in precisely copying the actions of both conspecifics and humans (Herman 2002). However, an important note of caution here is that this capacity has principally been demonstrated in terms of the dolphins' existing repertoire of bodily movements. Social learning of relatively novel techniques of food-handling, for example, has yet to be demonstrated. A priority is thus to perform experiments of the kinds completed for apes and reviewed above, particularly to test the capacity to acquire and sustain alternative traditions in different groups (Whiten *et al.* 2005; Bonnie *et al.* 2006; Horner *et al.* 2007).

Whether the capuchin findings are consistent with our CIH is less clear. Although they display multiple traditions and are encephalized in terms of EQ (brain size relative to body size), they do not have absolutely large brains or high neocortex ratios and their social learning has for some time been characterized as minimal, rather than common and sophisticated (Visalberghi & Fragaszy 1990, 2002). However, more recent studies have indicated that monkeys may have more imitative capacity than earlier thought (Voelkl & Huber 2000), and studies with capuchins specifically have identified social learning (Custance *et al.* 1999), some including the sophistication of discriminating the value of specific outcomes of others' actions (Brosnan & de Waal 2004). An ongoing study by Fragaszy and colleagues (Fragaszy *et al.* 2004*a*,*b*, p. 255) provides preliminary experimental evidence of diffusion of alternative foraging techniques. Thus, capuchins may be better social learners than earlier research suggested. At the same time, the traditions so far described for them appear less elaborate than those of chimpanzees and orang-utans. While most of the dozens of traditions described for the latter can be described as behavioural techniques, many of the differences for white-faced capuchins listed by Panger *et al.* (2002) involve applying universally occurring techniques like *rub* and *pound* differentially to various food types at different sites. Descriptions of a number of more elaborate foraging techniques including tool use are emerging for brown capuchins (*Cebus apella*; Ottoni & Mannu 2001; Fragaszy *et al.* 2004*a*,*b*; Moura & Lee 2004), but these remain to be systematically compared across sites, as done for their white-faced cousins. In sum, the capuchin data cause some doubt about the generality and scope of the CIH, but much remains to be confirmed about the nature of their traditions and social learning to permit comprehensive comparisons of *Cebus* and the great apes.

Finally, we noted that although there is much evidence for social learning and traditions in birds, there is so far little evidence of complex culture as we defined it. Perhaps this is simply because nobody has seriously attended to the distribution of traditions in this manner yet (West *et al.* 2003). In addition, the specific question of how much Caledonian crow tool use depends on social learning really needs to be answered. In the meantime, we can refer only to Lefebvre & Bouchard's (2003) finding that the ratio of social learning to innovation was remarkably low in their bird database compared to what has been reported for primates. This is perhaps surprising given the several parallels that have been identified between manifestations of intelligence in apes and in some birds such as corvids (Emery & Clayton 2004). Lefebvre & Bouchard (2003) consider several potential explanations for the bird/primate contrast they identify, dismissing observer biases and other factors in favour of the fundamental difference in 'food-handling organs': beaks versus a pair of hands with multiple digits. Still, some birds have been shown to be good at social learning, extending to imitation; New Caledonian crows are skilled in the use of more than one tool-type; and corvids in general have displayed various forms of social cognition: these together suggest we ought to remain surprised if they do not exhibit multiple-tradition cultures. Is a higher absolute brain mass important to achieve this? Or might other aspects of avian sociality provide the key (Emery *et al.* 2007)? We hope further experiments and observations in nature will clarify how avian and other taxa relate to the larger patterns we have identified in this paper.

In conclusion, the emerging patterns in the recent research we have reviewed have led us to formulate an embryonic Cultural Inheritance Hypothesis, linking social intelligence and complexities of animal culture. This is not presented as a direct competitor to the MIH. Rather, we see the CIH as one manifestation of the MIH in its original, broadly framed sense. A graphic example of this is that the marked encephalization of the orang-utan has always been an anomaly in relation to the MIH when the hypothesis was tested using group size as the proxy for social complexity (van Schaik 2004), for these apes are typically associated with some of the most minimal social groupings among primates. By contrast, they are a perfect fit with the CIH, as illustrated in figure 1 and discussed in relation to several sections of this paper. Barrett & Henzi (2005) have recently advocated an expansion of our theories of animal social intelligence to encompass a broader range of cooperative phenomena than are connoted by the narrow sense of 'Machiavellianism', and the present issue continues to expand our theories and knowledge of social intellect in new directions. Exploration of the diverse manifestations of culturally related phenomena among animals likewise extends our understanding of the special implications of social intelligence in new and productive dimensions. The fact that so much of the material we have drawn on has been collated only in the last few years highlights not only the exciting large-scale patterns in nature we can now begin to discern, but also emphasizes how large are the gaps in our knowledge that beg to be filled for so many animal taxa, besides the small set we have been able to discuss in depth.

A.W. was supported by a Leverhulme Trust Major Research Fellowship during the writing of this paper. We are grateful for comments on an earlier draft of the paper by Nathan Emery, Lydia Hopper and especially Simon Reader.

ENDNOTES

[1] Recognizing that for some, the gap is so great that culture should be ascribed only to humans, we put culture in quotation marks in our title.

[2] Space limits force the omission of any detailed consideration of other kinds of links between social intelligence and culture. Notable among these are (i) evidence that, consistent with the MIH, social information such as gossip achieves higher fidelity social transmission (Mesoudi *et al.* 2006*a*) and (ii) there is increasing evidence in primates for cultural transmission of sociality, as in the example of an unusual 'pacific culture' among baboons (Sapolsky & Share 2004; de Waal & Bonnie in press).

[3] There has been much controversy over the potential utility of recognizing 'memes' as units of cultural transmission (Dawkins 1976; Aunger 2000). This has most preoccupied students of human evolution, but the specific set of traditions tabulated for apes (Whiten *et al.* 1999, 2001; van Schaik *et al.* 2003*a*) suggests that the notion of memes might gain better purchase in these simpler cases. However, animal culture research has only begun to wrestle with the 'demarcation issue' of how traditions should properly be circumscribed. If one community of chimpanzees uses hammer-stones to crack two different nuts and another does neither, is that a difference in two memes or one? The examples of 'pound' and 'rub' in table 2 further illustrate this difficulty. In general, we suggest the answer must be, by analogy with the gene, that a meme is whatever cluster of behaviour patterns is transmitted as a package, but comparisons surmounting this problem in animal culture research are in their infancy.

[4] Cognitively simple innovations are those that could arise by individual discovery, and where the animals must merely repeat such an act in the same particular context. For instance, an orang-utan producing a kiss-squeak vocalization could accidentally have had its hand or a leafy branch right in front of its lips, have noted the change in sound quality this produces, and subsequently deliberately reproduce these contexts in order to bring about the new sound. Cognitively complex innovations are defined as those that appear to require some causal inference and require some deliberate action, not likely to arise by accident. Tool-use techniques fall in this category. Cognitively complex innovations tend to require practice before individuals adopting them can use them productively. We list the variants and their categorization in the electronic supplementary material.

[5] Some of this difference is due to the high-average gregariousness of chimpanzee males (Boesch & Boesch-Achermann 2000) and the low-average gregariousness of flanged orang-utan males (van Schaik 1999). If the focus were on mothers, for whom no separate published numbers exist, the species curves would be closer together and the chimpanzee curve less steep. A focus on mothers would be warranted if it is assumed that most cultural variants are learned as mature individuals, although extensive social learning is possible in adolescence and adulthood, as confirmed in recent experiments (Whiten *et al.* 2005).

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