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The Animal Connection and Human Evolution

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A suite of unique physical and behavioral characteristics distinguishes *Homo sapiens* from other mammals. Three diagnostic human behaviors played key roles in human evolution: tool making, symbolic behavior and language, and the domestication of plants and animals. I focus here on a previously unrecognized fourth behavior, which I call the animal connection, that characterized the human lineage over the past 2.6 million years. I propose that the animal connection is the underlying link among the other key human behaviors and that it substantially influenced the evolution of humans.

The evolution of any species can be understood by first identifying unique or diagnostic characteristics of the modern species and then tracing their development through time. Traits that are ancient and continuous and that provide causal explanations for significant attributes of the species in question are likely to have played crucial roles during evolution.

Traits often considered diagnostic of humans and significant in their evolution are (1) making and using tools (Darwin 1871; Leakey, Tobias, and Napier 1965; Oakley 1967); (2) symbolic behavior, including language (Calvin 2002; Diamond 1992; Mithen 1996; Pinker 2003), art, personal adornment (Conkey 1983; White 1989), and ritual; and (3) the domestication of other species (Childe 1951; Clutton-Brock 1999; Ucko and Dimbleby 1969*a*, 1969*b*). I hypothesize that a fourth trait, the animal connection, is an equally important and diagnostic behavior of humans and that the animal connection unites tool making, symbolic behavior and language, and domestication into an adaptive package.

The animal connection comprises an increasingly intimate and reciprocal set of interactions between animals and humans (i.e., members of the genus *Homo*) starting ~2.6 million years ago (mya). The animal connection began with the exploitation and observation of animals by humans. Over time, regular social interactions were incorporated into the animal connection. This trait is expressed today in the widespread adoption, or cross-species alloparenting, of animals—including dingoes, possums, bandicoots, raccoons, deer, moose, bison, fruit bats, lizards, bears, tapir, monkeys, sloths, coatimundis, antelopes, zebra, tree kangaroos, rabbits, weasels, ferrets, rodents, and birds, cervids, felids, and canids of all types (Serpell 1989)—as members of the family. This adoption involves active nurturing and care; ethnographic studies and early travelers' accounts often report women breast-feeding young animals or prechewing food for them (e.g., Galton 1865; Guppy 1961; Titcomb 1969). Pets or livestock become companions and social partners and are regarded as members of the family (Harris Poll 2007). First, I briefly review the other three diagnostically human behaviors.

Tool Making and Tool Using

Tool making and tool using are much more complex behaviors in humans than in other animals. Humans make a vast array of tools and have made tools for ~2.6 million years (m.yr.; Semaw et al. 1997). The genus *Homo*, the earliest-known specimen of which is ~2.4 m.yr. old (Hill et al. 1992; Kimbel et al. 1996), is usually identified as the maker of the earliest flaked stone tools, although *Australopithecus garhi* and other hominins also inhabited Africa at the time (Delagnes and Roche 2005; Panger et al. 2002; Semaw 2000).

Early humans used stone tools repeatedly for carcass processing. Direct evidence of this function comes from cut marks, scraping marks, and percussion scars on bones from many different sites (e.g., Blumenschine 1995; Blumenschine and Selvaggio 1988; Bunn 1981; Bunn and Kroll 1986, 1988;

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Capaldo 1997; De Heinzelein et al. 1999; Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003; Oliver 1994; Potts 1988; Potts and Shipman 1981; Selvaggio 1998). The use of tools on plants seems likely (Panger et al. 2002; Plummer 2004), but minimal direct evidence supports this contention (Keeley and Toth 1981).

Tool using in the broad sense is an extrasomatic adaptation (White 1959) of humans: a means by which humans evolved behaviorally without adapting physically. Tool use is a predominant, universal, and daily aspect of present human life, implying that the adaptive advantage of tools has been greater to humans than to apes.

Among nonhuman mammals, tool use is less complex and less frequent. Modern chimpanzees are the most adept animal tool makers and produce the largest tool kit. Chimpanzees make and use nests; termiting or anting implements; leaf sponges; hammerstones and anvils for breaking nuts; and sticks to pick marrow from bones, to dig for underground storage organs (e.g., tubers), and to locate and extract bush babies from tree hollows (e.g., Boesch and Boesch 1990; Goodall 1964; Hernandez-Aguilar, Moore, and Pickering 2007; McGrew 1992; Nishida and Hiraiwa1982; Pruetz and Bertolani 2007; Whiten et al. 1999; Yamamoto et al. 2008).

Captive but not wild bonobos make flaked stone implements (Savage-Rumbaugh and Lewin 1994; Schick et al. 1995; Toth et al. 1993). Nut-cracking chimpanzees produce archaeological sites with broken and chipped stones (Mercader et al. 2007), but their artifacts do not mimic the deliberately flaked stone tools of the Oldowan industry (Delagnes and Roche 2005). Although apes apparently possess the requisite cognitive and physical abilities for tool making (McGrew 1992:218), their performance as makers of stone tools and metatools falls short of early human behavior.

The importance of tool use in chimpanzees varies. Chimpanzees at Mahale spend little time ant fishing (∼1%–2% of the daylight hours) and gain little food (0.6 g protein; Nishida and Haraiwa 1982). However, Taï chimps spend hours cracking nuts and gain as much as 3,000 calories/day in season. Excluding nut cracking, Taï chimpanzees use a tool only every second day (Boesch and Boesch-Achermann 2000).

Significantly, humans use tools for different purposes than do nonhuman primates. Ape tools are rarely involved in killing or obtaining meat (Stanford 1996; Whiten et al. 1999). The main exceptions are bush baby spearing and marrow picking by chimpanzees and fish spearing. Bush baby spearing was observed 22 times in a single population (Pruetz and Bertolani 2007) and occupied, on average, ∼5 min/day. Spearing is used to locate and immobilize the bush baby, not to kill or dismember it. Sticks are also used to extract marrow from broken bones but not to break bones. Both bush baby spearing and marrow picking seem functionally similar to using sticks to extract honey from bees' nests (Boesch and Boesch-Achermann 2000). From the beginning of tool making, humans have been unique in flaking stone to make tools, in producing complex tools, in creating metatools, and in using tools habitually to obtain animal resources.

Symbolic Behavior

Following others (Henshilwood 2007; Henshilwood and Marean 2003; McBrearty 2007; McBrearty and Brooks 2000), I cluster symbolic traits together. Many are proposed signatures of behavioral modernity, including ritual, language, art, objects of personal adornment, and the use of ochre and pigments (e.g., Bar-Yosef 1998, 2002; Klein 2000; Mellars 2006; Mellars and Stringer 1989; White 1989).

Language, specifically, is widely considered a primary hallmark of humanity (e.g., Bickerton 1990, 2009; Corballis 1999; Diamond 1992; Dunbar 1996; Klein 2000; Pinker 1994). Full language confers a major adaptive advantage on a social species that relies heavily on information. For this reason, the distinctions between human language and communication among other animals have been studied extensively. q1

Language differs from other types of communication by its symbolic and reflective content, using arbitrary symbols (words) to convey meaning (Pinker and Jackendoff 2005). Language today involves syntax, grammar, lexical items (which refer to concrete objects, perceptible attributes, or actions), and disambiguators or grammatical items that permit humans to express complex relational or referential ideas and to speak of the past, the present, the future, and the hypothetical (Chomsky 1965, 1975; Hauser 1996; Jackendoff 2002; Jenkins 2000; Lenneberg 1967). Syntax and grammar distinguish true language from other types of communication but may not have been present at the origin of language (Pinker and Jackendoff 2005; but see Hauser, Chomsky, and Fitch 2002).

Any means of communication (including language) has the following three key components: (1) an audience to whom the communication is addressed, (2) a symbolic vocabulary shared by sender and recipient, and (3) a topic being discussed. Beyond these fundamental elements, full language is an enhanced and disambiguated form of communication.

Wild animals demonstrably communicate with each other. Vervet monkeys give different alarm calls to signal aerial versus terrestrial predators (Cheney and Seyfarth 1990). The symbolic vocabulary is clearly shared by the audience (the social group). However, the topic is not "snake" but "danger-snake"; the call cannot be used to ask the color of the snake, for example.

Animals in experimental situations are capable of fairly sophisticated communication. Educated apes use about 400 words, do not use syntax or grammar, and do not combine more than two or three words into sentences (Savage-Rumbaugh and Lewin 1994). One of the most linguistically adept nonhumans, Kanzi the bonobo, uses fewer than 400 words (lexigrams) but understands about 3,000 (Raffaele 2006). His performance is comparable to a human toddler's; at 30 months, toddlers have a vocabulary of ∼500 words (Fenson et al. 1994). The average high school graduate has a vocabulary of ~60,000 words (Hauser, Chomsky, and Fitch 2002), greatly exceeding ape performance.

Ritual, art, ochre, and personal adornment are used to transmit information about such concepts as beliefs, group membership, or style (Conkey 1983; White 1989), leaving physical manifestations visible in the archaeological record. Nothing interpreted as art, ritual, the use of ochre, or personal adornment has been reported in nonhuman mammals in the wild.

Domestication

Central to understanding the Neolithic Revolution (Bar-Yosef 1998; Binford 1989; Childe 1951, 1952; Klein 1995) is Childe's q2 hypothesis that domesticating plants and animals gave humans a revolutionary new control over their food sources. Domestication enabled humans to switch from foraging, hunting, and gathering to agriculture and triggered a shift from a nomadic or migratory lifestyle to settled living patterns.

Domestication itself is a process in which selective breeding by humans produces genetic change in a target species (Bökönyi 1989; Ducos 1989; Zeder et al. 2006*a*, 2006*b*). The process encompasses a spectrum of relations with target species, ranging from commensalism to situations in which humans have nearly complete control over the other species. The initial phase of domesticating animals is selecting for behavioral traits or "changing [the animal's] culture" (Clutton-Brock 1999:31–32). q3 Clutton-Brock defines culture as

> a way of life imposed over successive generations on a society of human or animals by its elders. Where the society includes both humans and animals then the humans act as the elders.

Only after fixation of behavioral traits are the morphological changes selected for, making the onset of domestication difficult to recognize.

At the heart of the process of taming a wild animal, bringing it into the household, and controlling its reproduction and genetic output over generations is the formation of an intimate, reciprocal, and individual relationship between a particular animal and a particular human (Clutton-Brock 1999). Forming a relationship with an animal is more akin to negotiating a partnership than to caretaking a plant (Budiansky 1992; Hearne 1994). Domesticating an animal is fundamentally developing a means of communication with that animal.

The ease with which zoonoses spread from domestic animals to humans shows the biological intimacy of the animal connection. For example, the Spanish flu epidemic of 1918–1919—the H1N1 viral strain (Taubenberger et al. 2005; Tumpey et al. 2005)—arose among domestic fowl or pigs, spread to their owners and handlers, and then infected and killed about 50 million humans. Offsetting such detrimental effects is the great advantage that accrues to having animals to perform labor and as food.

Domestic animals are recognized archaeologically by morphological changes, often including reduced body, tooth, and cranial size (Clutton-Brock 1999); changes in horn shape and size in sheep and goats (Shaffer and Reed 1972); appearance in a geographic region where wild ancestors are not known (Bibikova 1986; Wing 1972); changes in the demographic profile of animals, suggestive of slaughtering strategies (Zeder 2001, 2005, 2006; Zeder and Hesse 2000; Levine 1999); traits related to practices of keeping the animals, such as penning pathologies or dietary shifts revealed through isotope chemistry (Ervynck and Dobney 1999; Köhler-Rollefson 1989; Mashkour, Bocherens, and Moussa 2005; Pires-Ferreira, Pires-Ferreira, and Kaulicke 1976; Yuan and Flad 2002); the presence of structures or tools used in handling and keeping animals (Anthony 2007; Olsen 2003); burials; and genetics (e.g., Kadwell et al. 2001; Loftus et al. 1994; MacHugh et al. 1997; Parker et al. 2004; Verkaar et al 2004). Plant domestication is markedly different. Plants and growers do not have reciprocal, individual relationships. Humans select for specific plant morphologies and not for behaviors, except insofar as concerns a plant's ability to thrive. Seeds may be gathered, planted, watered, weeded, fenced, fertilized, protected, and the end product harvested with varying degrees of attention and diligence. The conditions of agriculture provoke a distinct evolutionary response from plants: Smith's (2006) adaptive syndrome of domestication, which favors plants with simultaneous seed maturation schedules, larger seed size, thinner seed coats, and less tendency for the seed heads to shatter spontaneously. Seeds of such plants are more likely to be harvested and stored for future planting and to mature more quickly once planted.

In the archaeological record, domestic plants are recognized by changes in seed morphology, by appearance in new geographic regions, and/or by genetic analysis. The apparatus of agriculture, such as ploughs, hoes, scythes, granaries, fields, fences, or irrigation ditches, leaves archaeologically visible traces. Other mammals are not known to domesticate plants or animals.

The Animal Connection as a Diagnostic Trait

Like the traits reviewed above, the animal connection is universal among humans, is capable of powerfully transforming behavior, and is absent or extremely rare among other species. The fundamental importance of the animal connection is exhibited in statistics on animal ownership in diverse countries. Annual expenditures are huge, such as $41.2 billion in the United States (American Association of Pet Product Manufacturers 2007), AU$4.62 billion in Australia (Australian Companion Animal Council 2006), L1.7 billion in the United Kingdom (Pet Food Manufacturers' Association UK 2008), $10 billion in Japan (Fackler 2006), and $870 million in China

(Chaney 2008). In both the United States and Australia, 63% of households include pets, compared with 43% of British and 20% of Japanese households. In the United States, the proportion of households with pets is larger than those with children. The number of dogs in Japan exceeds that of children under the age of 12.

Companion animals significantly affect and improve human health cross-culturally (Anderson, Reid, and Jennings 1992; Beck and Meyers 1996; Headey and Grabka 2007; Headey and Krause 1999; Headey et al. 2003; Serpell 1991). Pet-owning and pet-assisted therapies benefit handicapped, elderly, autistic, mentally ill, and criminal individuals (e.g., Chandler 2005; Cusak 1984; Fine 2006; Salotto 2001). Further, a truly enormous number of modern humans choose to live in intimate association with animals. Most livestock farms in the United States (98%) and China (96%) are family run (Hu and Zhang 2003; USDA Economic Research Services 2007, 2008). Animal products account for more than $100 billion per annum in the United States and ~$186 million in China (*People's Daily* Online 2005).

Same-species alloparenting is reasonably common among nonhuman primates (Maestripieri 2001; Stanford 1991; Thierry and Herrenschmidt 1985; Vasey 1997, 2007), but a search of the scientific literature turned up only one report of cross-species alloparenting in a wild primate: a capuchin monkey who nursed a marmoset (Izar et al. 2006). Nearly all reported cases of mammalian cross-species alloparenting involve human intervention (Mateo and Holmes 2004; Nature Australia 2002).

Numerous reports allege cross-species alloparenting of young humans by wild animals. Purported alloparents include wolf, bear, dog, gazelle, chimpanzee, vervet monkey, goat, sheep, cow, ostrich, jackal, panther, and leopard. Few written reports of feral children raised by other mammals (Gryce 2006; Itard 1962; Lane 1979; MacLean 1977; Malson 1972; Masters 2004; Osborn 2004; Reuters 2001; *The Scotsman* 2002) provide credible evidence of active nurturing, and often the children have not been seen in the company of the supposed alloparents. Rarely, children are seen feral dogs. q4 From this evidence, I conclude that adopting and nurturing individuals of another species is an extremely rare behavior among nonhumans, whereas the animal connection is a universal human behavior. In summary, the animal connection clearly is a universal human trait with a fundamental and enormous effect on human well-being.

The Hypothesis

I hypothesize that as an ancient, diagnostic trait of the human lineage, the animal connection had a major influence on human evolution, genetics, and behavior. This hypothesis predicts that the fossil and archaeological record will include abundant evidence that (1) humans were intimately and persistently connected with animals, (2) human adaptive changes were causally linked to the animal connection, and (3) a meaningful adaptive advantage of the animal connection can be identified in each stage of human evolution.

Below, I review the archaeological and fossil record in three broad chronological stages and discuss evidence related to my hypothesis. I focus on the following key adaptive transformations: the origin and evolution of tool making, the manipulation of symbols and origin of language, and the domestication of animals and plants.

The Early Stage: Inventing Stone Tools and Becoming a Predator

The early stage of the archaeological record encompasses a time from ~2.6 mya up to ~200,000 years ago. Tool making is the first diagnostic human behavior to appear in the archaeological record (Gona, Ethiopia, ca. 2.6 mya [Semaw et al. 1997]; Bouri, Ethiopia, ca. 2.5 mya [De Heinzelein et al. 1999]; Lokalalei, Kenya, ca. 2.4. mya [Roche et al. 1999]). This earliest industry is the Oldowan, or Mode I. The tool makers were early members of the genus *Homo* (Klein 2000) and possibly also members of the genus *Australopithecus* (Delagnes and Roche 2005; Panger et al. 2002; Potts 1991; Semaw 2000).

Several studies with broadly similar conclusions establish the function of Oldowan tools. Analysis of fossils at six sites at Gona (Domínguez-Rodrigo et al. 2005) and 400 specimens from Bouri (De Heinzelein et al. 1999) reveal cut marks, chopping marks, and percussion marks, indicating that processing animal carcasses was an important function of the earliest stone tools. Analysis of 2,700 fossils from 10 sites from Bed I, Olduvai (Shipman 1986*b*), revealed that (1) the frequency of flakes at these sites was significantly correlated with the frequency of cut marks on the fossils, (2) cut mark frequency was randomly distributed across bovids of all size classes, and (3) the frequency of cut marks on different skeletal elements was nonrandom and was highest on skeletal elements of the elbow (humerus or radioulna; see also Bunn 1981, 2001; Bunn and Kroll 1986; Shipman 1986*a*). Studies of early stone tools from Koobi Fora, Kenya (Keeley and Toth 1981), and bones from Swartkrans, South Africa (Pickering et al. 2006), also produced clear evidence of carcass processing. In summary, there is abundant, direct evidence that stone tools were used from the time of their invention to process animal carcasses (Harris and Capaldo 1993; Jones 1980; Schick and Toth 1993; Shea 2007; Stanford and Bunn 2001).

Either scavenging or hunting animals placed *Homo* in the predator guild, competing directly with carnivores (Blumenschine and Pobiner 2006; Bunn 2006; Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003; Shipman and Walker 1989). Stone tools gave humans a significant advantage by minimizing the time spent in interspecific competition over carcasses. Increasing the amount of meat in their diet (Aiello and Wheeler 1995; Shipman and Walker 1989) moved humans into a new, predatory ecological niche. However, predators must live at lower population densities than herbivores, leading to the prediction that this trophic shift should trigger either a dramatic drop in population density or a dramatic increase in geographic distribution (Shipman and Walker 1989). As predicted, the fossil record reveals that early *Homo* underwent a massive expansion of geographic range, moving out of Africa through the Levant and into Eurasia at about 2 mya.

Dmanisi, Republic of Georgia, preserves numerous remains of humans and other mammals at ~1.77 mya, shortly after this expansion (Gabunia and Vekua 1995; Gabunia et al. 2000; Lordkipanidze et al. 2005; Vekua et al. 2002). Tappen et al. (2007) found that most animals excavated at Dmanisi were Eurasian in origin or had migrated out of Africa long before 1.77 mya, leading them to conclude that the expansion of humans into Europe was not part of a generalized outflow of species from Africa but was caused by some factor specific to *Homo*, such as a trophic shift to a more predatory lifestyle.

Independent evidence of early human diet comes from genetic study of human-specific tapeworms (Hoberg et al. 2001; Shipman 2002). On the basis of mitochondrial DNA, two closely related species of *Taenia* specific to humans, *Taenia saginata* and *Taenia asiatica*, diverged between 780,000 and 1.71 mya, implying that their last common ancestor lived in early humans. The third human-specific tapeworm, *Taenia solium*, is genetically closest to tapeworms with end hosts among modern brown hyenas, spotted hyenas, African hunting dogs, lions, cheetahs, and jackals. Humans acquired these tapeworms by competing with African carnivores for the intermediate hosts, African herbivores.

The consilience of different types of evidence about the use of Oldowan stone tools is striking. A key consequence of the predatory niche of tool-making humans was that focusing on the behavior of prey (in order to obtain more food) and that of predators (in order to minimize interference competition) became adaptively advantageous. This marks the beginning of the animal connection.

An alternative interpretation of this time period is offered by Wrangham (2009) and others (O'Connell, Hawkes, and Blurton Jones 2002; Wrangham et al. 1999; see also comment by O'Connell, Hawkes, and Blurton Jones in Wrangham et al. 1999:581–582), who have hypothesized that consuming cooked tubers gave humans more energy to hunt and scavenge. Although cooking makes the nutrients in tubers more accessible, other predictions of this hypothesis (i.e., woodworking, digging sticks, and controlled fire at ~1.9 mya) are lacking (Bunn 2006).

The Transitional Phase: Becoming a Proficient Hunter and Communicating Information

The second stage occurred between ~200,000 years ago, when anatomically modern humans first appeared (McDougall, Brown, and Fleagle 2005), and ~40,000 years ago. In this stage, humans developed more sophisticated tool-making techniques, exploited a wider range of raw materials, and used tools for more specialized purposes. Heightened technological complexity was accompanied by a broadening of animal resources, including aquatic foods, fowl, and big game. These behaviors are used as indicators of behavioral modernity, along with the creation of art, language, ritual, objects of personal adornment, and the use of pigments.

When, and how, modern behavior arose is hotly debated. The traditional view is that behavioral modernity lagged significantly behind anatomical modernity (e.g., Bar-Yosef 1998; Binford 1989; Childe 1951, 1952; Dibble 1989; Klein 2000; Mellars and Stringer 1989; Mithen 1996, 2006), with a human revolution in behavior between 50,000 and 40,000 years ago. A few mutations, probably in brain function and/or language, may have enabled these developments (Diamond 1992; Klein 2000).

Recently, McBrearty and Brooks (2000) demonstrated that these modern behaviors appeared piecemeal in Africa before 50,000 years ago. They interpret behavioral modernity not as a single package that appeared suddenly but as an accumulation of behaviors over time (see also Bednarik 1994; Henshilwood 2007; Henshilwood and Marean 2003). Henshilwood and Marean conclude:

> Modern human behavior is defined here as behavior that is mediated by socially constructed patterns of symbolic thinking, actions, and communication that allow for material and information exchange and cultural continuity between and across generations and contemporaneous communities. The key criterion for modern human behavior is not the capacity for symbolic thought but the use of symbolism to organize behavior. (Henshilwood and Marean 2003:635)

Externally stored symbolic information is readily recognizable in the archaeological record and, in Africa, occurs well before 50,000 years ago. Pigment was used more than 300,000 years ago at Twin Rivers, Zambia (Barham 2002), and at Kapthurin, Kenya, ~282,000 years ago (McBrearty 1999).

The earliest ritual behavior might be the defleshing of the Bodo skull (~600,000 years ago; White 1986), though the defleshing and curation of a child's skull and cut marks on two adult skulls at Herto Bouri ~155,000 years ago are more compelling (White et al. 2003). Human and animal bones were cut and burned at Klasies River, South Africa, ~124,000 years ago (Singer and Wymer 1982), and Border Cave, South Africa, yielded an infant buried with a shell pendant and ochre at about 90,000 years ago, suggesting ritual treatment (Deacon and Deacon 1999).

Beads occur in Algeria and Israel at ~135,000 years ago (Vanhaeren et al. 2006); in Blombos Cave, South Africa, at ~75,000 years ago (Henshilwood et al. 2004); in Mumba Cave, Tanzania, at ~52,000 years ago (McBrearty and Brooks 2000); and in Elnkapune ya Moto, Kenya, at 40,000–37,000 years ago (Ambrose 1998). Personal adornment strongly suggests an awareness of self and of individuals outside one's social group (Kuhn and Stiner 2007).

Other evidence—big-game hunting, the use of marine resources and fowl, and the making of sophisticated tool kits including blades and bone tools—is documented at numerous sites older than 50,000 years ago (Backwell, d'Errico, and Wadley 2008; Bednarik 1992; Henshilwood et al. 2002; Marean et al. 2007; McBrearty and Brooks 2000). Although no single site necessarily contains all of the criteria of behavioral modernity, the African record strongly supports the contention that the human revolution did not occur abruptly.

In this second phase of human evolution, the cultural and biological importance of gathering and remembering detailed information about animals clearly racheted up. The most striking evidence of the growing importance of information about animals comes from prehistoric art.

Geometric markings occurred as early as 77,000 years ago but are difficult to interpret. More accessible figurative art became widespread in Africa, Europe, Asia, and Australia at ~40,000 years ago.

Prehistoric art can be regarded either as a sort of language—the external storage of symbolic information (Donald 1991)—or as evidence of full language (Noble and Davidson 1996), with an audience, a shared symbolic vocabulary, and a topic. The intended audience is difficult to pin down, but the symbolic vocabulary and, especially, the topic are obvious. Prehistoric figurative art uses a vocabulary of realistic images of animals, the vast majority of which are identifiable to modern viewers. Artistic renderings depict not only gross morphology but also coat color, posture, behaviors, sexual dimorphism, and mating stances.

The main topic of prehistoric art was undoubtedly medium to large animals, the most abundantly depicted subject during this period (M. Conkey, personal communication, 2008). Among the oldest figurative depictions is the parietal art of Chauvet Cave, France, now dated to 36,000 years ago (Bard, Rostek, and Ménot-Combes 2004; Mellars 2006), showing rhinoceroses, horses, lions, bears, mammoths, an owl, and handprints (Valladas et al. 2001). Carved ivory figurines of a lion-human chimera, a waterbird, and a horse from Hohle Fels Cave, Germany, are ~34,000 years old (Conard 2003). Art mobilier from between 25,500 and 27,500 years ago at Apollo 11 in Namibia (Wendt 1976) also depicts animals.

What is not depicted in any recognizable fashion is also key: there are no landscapes, no depictions of geographic features (mountains, water sources), no dwellings or shelters, and nothing about climate or weather. Rarely depicted subjects include humans, insects, small animals, birds, plants, reptiles, nuts, fruit, berries, or tubers (Bahn and Vertut 1999: 156). Thus, the overwhelming frequency of animal depictions, coupled with the expanded exploitation of animal resources, indicates the increasing value of the animal connection.

Producing prehistoric paintings cost time, energy, and resources. Pigments were gathered or mined, transported, ground, mixed with binders, put into containers of some sort, and applied with specially made tools. Oil, fat, lamps, and torches were expended to light cold, dark caves. Further, artists may have needed to be supported by others. These costs show that humans who occupied a cognitive or informavore niche (Miller 1983; Pinker 2003; Tooby and DeVore 1987) benefited greatly from enhanced means of recoding and communicating information.

The dominance of depictions of animals in prehistoric art suggests that the advantages of the animal connection may have driven the development of figurative art and language. Though Dunbar (1996) argues that language arose to communicate about human interactions, the earliest external documentation of information rarely includes human interactions.

The first and second stages of human evolution reveal a trajectory in behavior that is marked by an intensifying focus on the behavior and ecology of animals, accompanying a progressive broadening of the human predatory niche. When joined by increased sophistication in tool making, the animal connection enabled some human populations to procure more animal resources from a wider range of species and habitats—an obvious evolutionary advantage. Knowledge of the animals without the tools, or possession of the tools without the knowledge of the animals, was unlikely to have been advantageous.

The Final Phase: Domestication and the Invention of Living Tools

In the final phase, from ~40,000 years ago until the present, humans domesticated plants and animals, with highly visible and advantageous results. Childe (1951, 1952) hypothesized that the domestication of plants and then animals at about 12,000–10,000 B.C. caused the Neolithic Revolution (Clutton-Brock 1989; Flannery 1973; MacNeish 1992; Reed 1977; Smith 1995; Ucko and Dimbleby 1969*a*, 1969*b*) and that control over food resources was the key advantage of the revolution. q5

Recent findings by Germonpré and colleagues (2009) undercut this hypothesis. Evidence of a domestic dog nearly 32,000 years ago from Goyet Cave, Belgium, destroys the rough synchronicity of the domestication of plants and animals. The Goyet dog is at least 17,000 years older than the next-oldest domesticate (also a dog) and 21,000 years earlier than the oldest domesticated plant (rye at Abu Hureyra; Moore, Hillman, and Legge 2000). Contrary to predictions of Childe's (1951, 1952) hypothesis, the earliest domesticates are dogs, which are eminently unsuitable as stock animals (Diamond 1994:169). These animals were not processed for consumption, and at the outset, domestication was not designed to gain control over food resources.

Why were animals domesticated first? The animal connection hypothesis predicts that animals were domesticated first because their treatment was an extension of tool making, the primary adaptation of the first phase of human evolution, and gathering knowledge about animals, the primary adaptation of the second. I argue that the real advantage of animal domestication is using animals as living tools that also provide valuable renewable resources.

At least 10 such resources can be identified as follows: (1) muscular power beyond human strength; (2) rapid transport of goods or people; (3) raw material (wool or hair) for making fabric, rope, and so on; (4) useful fertilizer, fuel, and building material (manure); (5) free disposal of refuse and ordure; (6) mobile wealth and storage for excess grain crops (which can be retrieved via slaughter); (7) high-fat and high-protein food (milk and milk products) for adults and weanlings, enabling a decrease in interbirth spacing; (8) protection for people, possessions, and dwellings; (9) tracking and killing of game or pests; and (10) combined traits that enable humans to live in new habitats. Examples of the last resource include the advantages camels offered in deserts, pigs and dogs in Oceania, reindeer and dogs in the Far North, yaks in the mountain regions of Asia, and alpacas and llamas in high-altitude South America.

In essence, domestic animals are another kind of extrasomatic adaptation or tool that expands the resources humans can exploit. Transferring the concept of tool making and tool using from inanimate stone or wood to live animals was a fundamental advance in human evolution predicated on knowledge of biology, ecology, physiology, temperament, and intelligence of target species; of the selective breeding; and of communication techniques based on the animal connection.

Galton (1865) suggested that the domestication of animals arose from the human tendency to adopt wild animals (the animal connection), a thesis I and others support (Clutton-Brock 1999; Serpell 1989). I argue further that the intensive observation, handling of, and intimacy with wild animals in the first two stages of human evolution were the essential prerequisites to domesticating and using animals as tools.

Clearly, humans who handled and lived with animals more successfully accrued a selective advantage in performing tasks that humans without animals could not achieve. Domestication was reciprocal, as the animals in turn selected for behavioral or physical traits in humans, such as better communication with animals and the continued functioning of lactase into adulthood. Lactase enables adult humans to eat milk products without gastric distress. The underlying mutations arose at least twice among cattle-herding people in the past 10,000 years (Burger et al. 2007; Durham 1991; Enattah q6 et al. 2002; Tishkoff et al. 2007), showing its importance.

In this phase, the animal connection gave a selective advantage to humans who had better abilities to observe, to draw conclusions, to communicate, and to make a new sort of living tool. These abilities preadapted humans to live in higher densities and more permanent settlements, as happened once domestication of plants and stock animals occurred.

Conclusion

In this review, I define a unique human behavior, the animal connection, and call attention to its deep roots. My hypothesis is supported by abundant evidence of the animal connection and its increasing importance through time.

In the first phase, the earliest function of tools was to improve human access to animal foods, thrusting humans into a new ecological niche. In the second phase, the earliest evidence of external storage of information concerned animals. Symbolic behavior and communication provided key benefits as humans expanded into new geographic ranges, developed more sophisticated tools, and broadened their niche. In the third phase, domestication provided niche-changing benefits to those humans who were able to communicate well enough to make living tools out of animals. In each phase, early and fundamental advantages accrued to those who were more animal focused.

The animal connection hypothesis highlights causal links between tool making and the origin of symbolic behaviors (including language) and from those to the domestication of animals and plants. These seemingly different behavioral advances were intimately intertwined during human evolutionary history.

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True to form, this paper represents yet another significant contribution by Pat Shipman. In it she proposes a thought-provoking new theory of human evolution, based on what she calls the animal connection, one of four behaviors used to characterize the human lineage. The other three are tool making, symbolic behavior and language, and domestication.

She proposes that the animal connection is the underlying link among the other key human behaviors and that it substantially influenced the evolution of humans. While providing a clear list of features that distinguish humans from other animals, Shipman at once attributes uniquely human behavioral traits to the long and intimate relationship they share. On the basis of a review of the archaeological record, the author provides good evidence in support of her theory.

Identifying four behaviors unique to humans is a welcome move by Shipman in a time replete with unresolved arguments about degree of capability, origin, and timing of various events and exactly which hominin taxa are in or out. As a starting point, a major issue that complicates characterizing the human lineage is a lack of consensus among scholars on the definition of intelligence, especially when applied to nonhuman primates. Given the complex tool-use behavior in other animals, including birds, is not the level of sophistication we see in human tool use only by degree? Innovative tool use, from its early inception, appears sporadically in the archaeological record in geographically disparate regions among different hominin taxa, indicating that it was not a gradual process that proceeded in parallel with hominin behavioral evolution. We wonder whether the discontinuity was culturally, climatically, demographically, or geologically controlled. The stone tool record evidences vast periods of stasis, punctuated with innovations that were sometimes later lost, telling that human evolutionary behavior does not fit perfectly into an ordered chronological event. The precision grip in *Paranthropus robustus* presents an interesting example of a taxonomic quandary when it comes to identifying behaviors unique to humans. While found in higher apes in degrees significantly more restricted than in humans, evidence of a precision grip is considered a human trait synonymous with tool use. In addition, the highly derived dentition and sagittal crest are widely accepted as evidence of dependence on a specialized vegetarian diet. However, isotopic analysis of *P. robustus* remains shows that they consumed an anomalously high amount of protein. Our research on bone tools associated with *P. robustus* at three sites in South Africa, together with microscopic analysis of experimentally created wear patterns, suggests that these bone tools were likely used to process fruits, dig for underground storage organs, and extract protein-rich termites from their mounds. Taphonomic analysis of associated faunal remains shows that bone of a specific type and size was intentionally selected for use as a tool, and robust pieces from two sites demonstrate that the users occasionally modified the ends of implements through grinding to obtain optimal efficiency in the tasks for which they were used. If we consider problem-solving food acquisition as an indicator of intelligence, then it would be fair to conclude that *P. robustus* was a tool-using, cognitively advanced omnivore, like *Homo*.

In light of the few considerations mentioned, Shipman was wise in identifying four main traits as diagnostic of humans. In accordance with these, she is able to convincingly incorporate archaeological evidence of a unique long-term relationship between humans and animals, supporting the theory that this association, which assumed different forms, was ultimately a driving factor in the evolution of traits specific to humans. Having been alerted by Shipman to the very real link between hominins and other animals, it occurs to us that this connection forms part of a larger relationship with nature, including insects, plants, rocks, water, and other elements in any given ecosystem. In this regard, connections with animals may have been a successful momentary strategy (as with other behaviors) to fulfill very different needs without necessarily having been a continuous process characterizing the evolution of humans. An alternative scenario is that the hominin lineage, including modern humans, is characterized by an ability to be increasingly successful predators that shift to other resources when necessary.

We foresee that the previously unrecognized connection between humans and animals will become established in literature on human behavioral evolution and congratulate Shipman on identifying this age-old link. We anticipate that the model will evolve to include a broader view of chimpanzee and other animal cognition, behavior, and technology. We feel that the current division into four behaviors paints too linear a perspective of hominin cultural evolution and would benefit from a less biologically dependent view on the origins of language and symbolic behavior, given that Neanderthals used personal ornaments made of animal teeth and buried their dead in association with faunal remains.

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Humans, as the animals they are, are intimately connected with the animal world to which they pertain. Shipman presents an interesting idea, which is that this connection has shaped our evolution in the past 2 million years. Animal connection (AC) would explain (or is behind) the emergence of stone tool use, language/symbolic behavior, and domestication. As interesting as this idea is, there are some observations that need to be considered when taking AC as a working hypothesis.

There is a concern among philosophers of science about the inaccurate use of the terms “hypothesis” and “theory” by anthropologists (see Bunge 1998*b*). Theories should be based on a hierarchical system of hypotheses. Scientific hypotheses should then be articulated around well-defined (i.e., exempt of ambiguity) and contrastable premises. Failure to do so leads to the perception that the typical research project in anthropology is a fact-finding mission (Bunge 1998*b*). The premises of AC, as outlined by Shipman, are missing a connection between their conceptual content and their contrastability. This differentiates theoretical or founder hypotheses from what Bunge (1998*a*) defines as factual hypotheses, which are the ones determining the heuristic potential of any given theory.

I share Shipman's belief that there is a clear connection between human evolution and animal exploitation, but I would be hesitant to refer to animal consumption as AC. The connection between hominin evolution and AC in this regard would be similar to, let's say, the evolution of other carnivore species and their consumption of prey; that is, either prey change and predators need to readapt (following a "Tom and Jerry" effect) or predators evolve and modify their predatory niche (through the evolution of their specific predatory range). Other carnivores would also have an AC. The only difference with this comparison that Shipman introduces here is that in order to consume animals, humans must process them first with the aid of stone tools. Therefore, the emergence of stone tools in human evolution was triggered by the consumption of animal food and, hence, by AC. Shipman uses as empirical support of this assertion the identification of a variety of percussion and cut marks on bones from six sites in Gona and 400 bones in Bouri dating to circa 2.6 Ma.

However, it should be emphasized that archaeologists are not in an epistemically reliable position to claim that stone tool emergence was caused by meat eating alone or that meat eating was the main reason, as has been traditionally defended. If we consider the raw evidence, for the first 600 ka of the archaeological record before 2 Ma, archaeologists have only very scanty evidence of stone tool use and carcass processing: only slightly more than a dozen elements have been documented to bear cut marks (Domínguez-Rodrigo 2009).

Most of the earliest sites have no fauna or very few faunal remains associated with the stone tools. Poor preservation of bone cannot be argued to be the reason. Volcanic rocks are very sensitive to environmental and depositional conditions. Subaerial weathering caused by exposure or chemical weathering by soil properties impacts volcanic rocks conspicuously. Most of the early Gona sites where fauna is not documented show excellent preservation of lithics, which discards the hypothesis that the absence of bone is due to diagenesis.

Likewise, more recent analyses of the Oldowan stone tool kit from Olduvai Gorge show that flake number and cut-marked bone frequency do not correlate, first, because several artifacts previously identified as flakes are described as by-products of battering activities (Mora and Torre 2005) and, second, because there is no taphonomic evidence that such battering activities were aimed at breaking open marrow-bearing bones (Domínguez-Rodrigo, Egeland, and Barba 2007). As an example, at FLK North 1-2 a few hundred flakes were discovered, and only 21 bone specimens can be argued to bear unambiguous cut marks. There is mounting evidence that the Oldowan kit at several Olduvai Bed I and II sites may reflect other activities by hominins nonrelated to carcass exploitation. Plant connection may be as important as or even more important than animal connection during the first half-million years of stone tool use.

Shipman rejects this idea by mentioning that there is minimal evidence of this. However, Keeley and Toth's (1981) paper, which she uses as support, shows that there are more plant/wood use wear polishes on the tools analyzed than meat polish, despite the small sample size.

Early Pleistocene hominins were eating meat, as documented in the anatomically patterned distribution of cut marks (the elbow being roughly as cut marked as the posterior zygopodes, especially in smaller carcasses). The long bone portion distribution of cut marks provides overwhelming evidence of defleshing over other carcass-processing activities. However, if this is the only evidence of AC for more than 2 million years, it certainly cannot be claimed to be a distinctive feature of *Homo*, probably until much later in its evolution, when AC can be archaeologically detected in exclusively human characteristics such as iconography, broad-spectrum hunting, and, eventually, domestication.

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Shipman accurately considers the animal connection as a form of behavior that, along with tool making, symbolic behavior, and the domestication of plants and animals, helps to distinguish humans from other mammals. Shipman surmises that the appeal that animals have for humans probably finds its source in the beginning of meat eating on the African savannah more than 2 million years ago. The processing of the carcasses with stone tools and the understanding of prey through observation entailed a profound knowledge of animal anatomy and behavior, respectively. The appearance of the first anatomically modern humans (AMHs) in Africa coincides with the recurrent evidence of the use of objects in the symbolic realm, as discussed by Shipman.

Shipman links the capturing, taming, and raising of animals to the animal connection. Adoption of wild animals probably happened persistently from the Paleolithic until historical times for several reasons (keeping animals as pets, using them to carry burdens, using their fur, or using them in rituals; Drucker 1951; Kwon 1998; Pisudski 1998; Serpell 1989; Simoons and Baldwin 1982; Stefansson and Wissler 1919). Shipman surmises that the animal connection hypothesis would motivate humans to domesticate them to be used as living tools. In addition, I think that animals were also seen as vessels of symbolic meanings and that their presence enabled ritual performances. The ethnographic record on circumpolar hunter-gatherers delivers numerous examples. The Sami wore perforated bear canines as protection against bear attacks (Itkonen 1946). Inuit shamans attached metatarsal bones of foxes or wolves to their belt to ensure strong legs and speed (Issenman 1997). Koyukon people raised hawk owls so that their children could become as fastidious and as good of a hunter as the bird (Nelson 1983). Paleolithic art hints at the symbolic importance of Pleistocene mammals. According to Vanhaeren and d'Errico (2006), Aurignacian people expressed their group identity through visual clues such as personal adornment. In Northern Europe, these ornaments are especially composed of perforated fox, wolf, and bear canines. Decorated wolf/dog metapodials and copies of these bones carved out of mammoth ivory point to the symbolic significance of the wolf/dog for the Gravettian people of Avdeevo (Russia; Gvozdover 1995).

Tamed born-wild animals that were kept captive would be suitably available for ritual/ceremonial purposes (Simoons and Baldwin 1982). The ethnographic literature offers various cases. Some native people, such as the Ainu, raised captured bear cubs. When the cub became adult, it was ritually killed at a communal feast so that its spirit could be sent back to the land of the gods. In return, the gods replenished the human world with spiritual and material resources (Akino 1999; Kimura 1999). The Ainu believed that the spirit of the animals resided in the skull, and during the ceremony, they made a hole in the braincase so that the spirit might be released. The Ainu used not only captured bears in their sending-away ceremonies but also foxes and wolves, sometimes raised as pups (Pisudski 1998; Walker 2005). Bear ceremonialism, which in most cases is related to the killing of a wild bear, is widespread throughout northern hunting societies (Hallowell 1926). Furthermore, evidence exists that a protobear ceremonialism originated during the Upper Paleolithic (Germonpré and Hämäläinen 2007).

However, taming an animal does not make it a domesticate (Schwartz 1997). Serpell (1989) argues that Paleolithic groups did not undertake the arduous task of breeding tame animals in the absence of economic or ecological pressures. However, the beginning of dog domestication could have been initiated by symbolic or ceremonial necessities. Circumstantial evidence suggests that out of stocks of captive wolves, which were kept for purposes of ritual, the most docile and communicative animals were selected to breed, resulting, after a number of generations, in primitive dogs. The Goyet dog skull, which is nearly 32,000 years old, indicates that as early as the Aurignacian, AMHs already possessed dogs (Germonpré et al. 2009). The Goyet skull does not display any sign of specific human handling. However, some 40% of the canid skulls from the Gravettian Předmostí site (Czech Republic) have perforated braincases, suggesting a ritual treatment of these carnivores (M. Germonpré, unpublished data). Also, one of the dogs from the Epigravettian Eliseevichi site (Russia) had a perforated braincase (Sablin and Khlopachev 2002). q18

Even so, a ritual/symbolic approach to the origin of dog domestication does not preclude the idea that the dog was not important as an extra tool. As noted by Shipman, and also by Crabtree and Campana (1987) and Clutton-Brock (1995), the first dogs could have been used in many ways, such as draft animals. Help with transport could even have offered an advantage to the Aurignacian AMHs over the Neanderthals and might even have been one of the factors in the demise of the Neanderthals. All in all, Shipman's animal connection hypothesis is very helpful for gaining insights into how Paleolithic people regarded Pleistocene animals.

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Anthropologists have long recognized that reliance on technology, symbolic behavior (especially language), and the domestication of other species are uniquely derived human traits. To these, Shipman would add the unique manner in which humans relate to other animal species, and she argues that this animal connection underlies the other more commonly recognized human traits. No one will dispute that human interaction with other species is distinctive, but we may disagree about whether it is the cause or the effect of other human behavioral distinctions. A case for effect may follow from the prehistory that Shipman summarizes, since those aspects of the animal connection that are most obviously unique—the domestication of various species and the incorporation of some species into human families or households—appeared mostly after 12,000 years ago. Only the special relationship between people and dogs may be significantly older, and almost everything about it, including its near ubiquity and its level of intimacy, suggests that it might be understood not so much from the human side but more from the dog's as the human connection.

Shipman takes a gradualist's view on the evolution of human behavior, and she accepts that Africans and perhaps other people before 50,000 years ago possessed the same capacity for the animal connection as people afterward. This would follow from sparse but now oft-accepted archaeological evidence for modern human behavioral markers in Africa before 50,000 years ago. Yet, however one evaluates this evidence, it remains true that human fitness—the ability to survive and reproduce—improved dramatically about 50,000 years ago. The clearest indication is the abrupt expansion of modern humans from Africa at about this time, but increased collection pressure on tortoises and intertidal shellfish suggests that Africans living under similar conditions were significantly more numerous after 50,000 years ago than before (Klein 2008). It seems reasonable to propose that whatever enhanced human fitness about 50,000 years ago also explains those aspects of the animal connection that are truly unique.

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Shipman's article makes a number of valuable points while summarizing the ever-changing and complex human-animal relationship. With considerable clarity, she describes the history of humanity as we accumulated the three essentials that propelled us down the road of evolution: tools, symbolic behavior, and domestic plants and animals.

It is possible to reiterate and support Shipman's arguments by highlighting any one of the animals brought under human control to the degree that they are ordained as members of the elite domestic cohort. In my research through the years on the human-horse relationship, all three of these stages are readily recognizable. Humans hunted horses in the Pleistocene for food via both stalking and organized communal hunts involving spears. The carcasses of these equine prey were then butchered with sharp blades, their hides scraped, and their bones converted into useful implements, such as needles and awls.

Paleolithic peoples applied their symbolic acumen in performing the necessary communication to plan, organize, and conduct repeated communal hunts such as those seen at Solutré, France (Combier and Montet-White 2002; Olsen 1989). The diversion of bands of horses into this natural corral for dispatching occurred during seasonal herd migrations for a span of more than 20,000 years. At least four different cultural traditions, the Aurignacian, Gravettian, Solutrean, and Magdalenian, adopted this hunting strategy. One can only speculate as to whether one culture passed it down to the next or each subsequent group reinvented it, seeing the piles of horse bones eroding out of the talus slope.

The Paleolithic hunters also chose to illustrate horses, as well as other prey, in cave paintings (Olsen 2003*b*; Guthrie 2006) and carved their effigies in ivory, antler, and bone (Olsen 2003*b*). Through their vivid portrayals, these early artists revealed their deep understanding of the species that sustained them. The horse's appearance, individual and group behavior, seasonal changes in pelage, and the ways in which they were hunted are all depicted.

After a great reduction in the range of wild horses transpired in the early Holocene, the Eurasian steppes became the primary domain of the tarpan. Ultimately, between about 4000 and 3500 BCE, nomads probably dwelling in Ukraine, Russia, or Kazakhstan succeeded in domesticating horses (Olsen 2003*a*, 2006*a*, 2006*b*). With domestication, horses served as a ready source of meat and milk (Outram et al. 2009), a means of transportation, and a supplier of fuel and insulation (manure), as well as hides, bones, and hooves (Olsen 2008; Shnirelman, Olsen, and Rice 2003).

Haulage by several species of domestic animals, whether by packs, sled, travois, or wheeled vehicle, revolutionized societies in countless ways. Admittedly, the multiplicity of uses of horses is greater than for most species, with chariotry and cavalry leading the charge in terms of their impact on world geopolitics. With the Industrial Revolution, the horse became an automated machine adapted to a wide array of uses based on this large beast's tremendous strength (McShane and Tarr 2007). Sports and leisure top the list of equine roles today in much of the developed world, but with equine-related therapy we see an even greater expansion of the roles of the horse in culture. It is clear that the final stage has yet to arrive for the human-horse relationship, even if equine numbers are declining today.

Shipman's assertion that the animal connection modifies human evolution is probably easier to comprehend at the inception of human history, since natural selection was likely more severe when the relationship involved seizing a carcass from a pack of hyenas or dispatching a mammoth. Both symbolism and technological innovation played a role in human evolution by enabling more humans to survive and reproduce. Those who could communicate better improved their odds considerably, as witnessed by the longevity of communal horse hunting at Solutré. Therefore, to the extent that tool use and symbolic behavior involve an animal connection, Shipman's argument is supported. On the basis of the massive volume of evidence, her point that animals played a pivotal role in the daily lives of ancient peoples is difficult to deny.

Arguably the strongest evolutionary impact that close contact with animals has had on humans was through the transmission of zoonoses (Barnes 2005; Torrey and Yolken 2005). Many of the most common and often virulent diseases that have threatened human survival can be traced back to probable origination in domestic animals, including measles (dogs), mumps (poultry), tuberculosis (cattle), and the common cold (horses). Likewise, the handling and consumption of wild species has transmitted other lethal diseases, including smallpox and HIV, both probably derived from African primates. Those humans that possessed a genetic predisposition to survive zoonoses contributed more offspring to future generations, demonstrating the evolutionary influence of the animal-human relationship.

In closing, it is important to remember that the human-animal relationship also impacts the animals' survival and adaptation. If human evolution is influenced by the relationship to animal species, the same can be said for the animals to which humans are connected, either via hunting or herding. It has been said, for example, that the horse was en route to its ultimate demise, that is, extinction, until it was rescued through domestication (Budiansky 1997).

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22 III 10

Sometimes it pays to state the obvious. I think that is largely the case with Shipman's paper, because in emphasizing the evolutionary importance of hominid-nonhominid interaction, she also provides a valuable review of some major ecological and behavioral connections between those biotic actors since 2.6 million year ago (Ma), the earliest-known date of a detectable archaeological record. Disagreements I have with Shipman's synopsis of those inferred linkages are so specific that dwelling on them in this short comment format would be pedantry.

I do, however, wonder why Shipman contends that the animal connection, "an increasingly intimate and reciprocal set of interactions between animals and humans," is a "unique or diagnostic" characteristic of the genus *Homo*. Yes, I can accept that hominid-nonhominid dynamics catalyzed the invention of stone tools (possibly by early *Homo*; but see De Heinzelin et al. 1999) and the emergence of symbolic behavior and domestication. But, of course, the hominid lineage evolved independently for many millions of years before those archaeological markers, after it split from the last common ancestor it shared with chimpanzees. During that long phase of evolution, these earlier hominids, like their lithic technology-possessing, symbol-using, domesticating descendents, surely had animal symbionts and competitors—as did/does nearly every other extinct and extant animal that I can imagine. The problem for paleoanthropologists is that we are currently unable to reconstruct many of the ecobehavioral dynamics of this interval because there is no archaeological record of the period from which to draw inferences about those dynamics. In other words, we can only conjecture that the animal connection of prelithic hominids was less (or, for that matter, more) "intimate and reciprocal" than that of the genus *Homo*.

For instance, it does seem likely that the reduced gut size of *Homo* (inferred from rib cage and pelvic morphology; Aiello and Wheeler 1995), compared to that of at least some earlier-known hominid taxa, required its increased reliance on high-quality, easily digestible foods such as meat. But, that does not mean, in direct opposition, that earlier or contemporaneous but differently derived hominids, with more capacious guts than possessed by *Homo*, were incapable of obtaining and/or eschewed meat as a regular food. First, stable carbon isotope analyses reveal probable meat-eating signatures in relatively primitive (*Australopithecus africanus*) and in highly derived (*Australopithecus robustus*) australopithecines (Lee-Thorp, van der Merwe, and Brain 1994; Sponheimer et al. 1999, 2006). Second, australopithecine fossils co-occur, nearly as often as do early *Homo* remains, with the earliest stone butchery tools, and australopithecines also presumably possessed the requisite hand anatomy to make and use those tools (e.g., Susman 1988). Third, chimpanzees, the closest-living relatives of humans, are avid hunters and meat eaters (reviewed in Newton-Fisher 2007). And, although recently published revelations about *Ardipithecus ramidus* locomotion (e.g., Lovejoy et al. 2009; White et al. 2009) serve as a general warning about pitfalls in cladistically based models of trait distribution, it is still plausible to hypothesize that hunting and meat eating are hominid-chimpanzee synapomorphies or symplesiomorphies. If true, it's easy to envisage—and model—nonlithic acquisition and processing of vertebrate carcasses by early hominids, who targeted small prey and used their hands, mouths, and perhaps perishable, organic tools to kill and render them into edible portions (Pickering and Domínguez-Rodrigo 2010). I stress that this is a hypothesis of regular meat eating, as distinguished from other models that posit no or just occasional ("marginal") meat eating by prelithic hominids. There is nothing in the morphology or about the inferred behavior of these taxa that precludes this possibility. (Based on their review of hominid dentognathic morphology and tooth wear, Teaford and Ungar [2000:13,510] argued that "australopithecines were not preadapted for eating meat," but how many meat-eating [pre-]adaptations are shown, for instance, in the skull and teeth of modern chimpanzees, known, regular meat eaters? In light of this example, as well as admissions from Teaford and Ungar that there are ways to reconcile a hypothesis of australopithecine meat eating with their morphologically/wear-analysis-based conclusion, their objection falls away.) Testing this hypothesis is a challenge in a strictly paleontological (nonarchaeological) 2.6-Ma record, but what is not a challenge in paleoanthropology?

To close, I note that butchery damage patterns—with cut marks on meat-bearing ungulate limb bones, the lingual surface of a mandible, and the ventral surface of a rib—in the 2.6–2.5-Ma Gona and Bouri archaeofaunas (De Heinzelin et al. 1999; Domínguez-Rodrigo et al. 2005) indicate early access and, by extrapolation, hunting and/or aggressive scavenging by hominids. We can infer from this that the emergence of efficient hominid carcass foraging was full-blown and instantaneous with the invention of stone tool technology. But, it's equally likely (and more plausible, to me) that hominids already long possessed the obligatory ultimate and proximate motivations, as well as the physical capabilities, for regular acquisition and eating of meat—and, thus, also well-developed, intimate, and reciprocal interactions with other animals.

Reply

Before addressing remarks by specific colleagues, I would like to thank those who commented on my article for their close attention to my ideas. Olson and Germonpré both make pertinent observations about the nature of human-animal interactions. Olson reminds us that such interactions influenced both human and animal evolution, in part through the transmission of zoonoses and in part through the dramatic changes that have been wrought through domestication. Both humans and their close animal companions may be regarded as having been domesticated.

Germonpré makes the equally powerful observation that domestication—particularly of dogs, which were domesticated so much earlier than other species (Germonpré et al. 2009)—may have yielded benefits in terms of both dogs' ability to be used as living tools and their ability to play significant symbolic and ritual roles. This observation applies to noncanids as well. Both potential tool use and symbolic value may have shaped the circumstances under which animals were domesticated. Both attributes may have provided motivation for taming and possibly domestication as well. I had underestimated the potential importance of the symbolic role of animals, and I thank Germonpré for bringing this to the fore.

Backwell and d'Errico suggest that I make a persuasive case that the evolutionary trajectory I call the animal connection had a strong influence on human evolution, which I appreciate. They observe that the effects of the animal connection may not have been steady or even continuous. I agree with them and regret that my summary of a vast body of evidence may have inaccurately implied that the animal connection evolved linearly. Linear evolution in complex behaviors is probably more often the exception than the rule.

Domínguez-Rodrigo and Pickering raise some points of disagreement or caution. The former misunderstands me to some extent, in that I do not think merely consuming animal flesh constitutes the special relationship I have called the animal connection. Were that true, then any species that ever engages in predatory behavior would have the same connection and the animal connection would be useless as an explanatory mechanism for the unique attributes of humans.

I do not claim that stone tool emergence was caused by meat eating alone, simply that the evidence at hand indicates strongly that the earliest stone tools were used in procuring animal resources. The evidence of earliest stone tool use is sparser than either Domínguez-Rodrigo or I would wish, but it is all the evidence we have. The absence of bones from many of the Gona sites strikes me as most probably the result of the many taphonomic events that degrade bones but not stone. If I understand Domínguez-Rodrigo correctly, he suggests that the lack of bones at early Gona sites might be due to the fact that the initial site formation activities did not involve bone. This is an interesting but difficult-to-test idea.

Both Domínguez-Rodrigo and I refer to information about stone tool use at Olduvai, an approach that has the immense benefit of huge sample sizes, so that analyses can be statistically meaningful—unlike information from Gona. Unfortunately, the evidence from Olduvai comes from sites that were made well after the earliest tools; the bottom of Olduvai Bed I is 1.9 m.yr. old. A similar problem besets the Keeley and Toth (1981) study of use-wear on 1.5-m.yr.-old stone tools from Koobi Fora. Only nine tools were successfully analyzed for microwear traces, and those were made more than 1 m.yr. after the Gona tools. Did the use (function) of stone tools remain static for a million years or more after their invention? Possibly, but we do not know this.

I do not suggest that early stone tools were used only for procuring meat or other animal resources. Other uses are possible and perhaps probable, but they are not proven. To assess the use of the earliest stone tools rigorously, we must weigh the oldest evidence more heavily than later evidence, we must be suitably cautious about small sample sizes, and we must be careful in applying conclusions from one time period to another. I am confident that Domínguez-Rodrigo would agree with these cautions.

Pickering raises other issues about the interpretation of the earliest uses of stone tools. He maintains that the cut marks on bones associated with the earliest stone tools show that "the emergence of efficient hominid carcass foraging was full-blown and instantaneous with the invention of stone tool technology." I am more cautious than he in interpreting these data. I suggest only that a significant increase in carcass foraging and processing occurred when stone tools were invented and that regular use of large animal carcasses would have inevitably put hominins into direct competition with the large carnivore guild. I also argue that because stone-tool-wielding hominins adopted large-animal predation as a major component of their subsistence strategy, this new ecological niche would have offered a considerable adaptive advantage to those hominins who increased the attention they paid to the habits of both other predators and prey.

I agree heartily with Pickering that prelithic hominins had animal symbionts and competitors, "as did/does nearly every other extinct and extant animal that I can imagine." In my view, what changed (increased) with the advent of stone tools was the ability of hominins to access significant quantities of animal resources, the average size of the animals they exploited, and the ecological and nutritional importance of animal resources in their lives.

Pickering suggests that chimpanzees engage in "regular meat eating," a term I would not necessarily apply to their behavior. Chimpanzee hunting and meat eating are certainly recurrent—and occur in several populations as often as once a week—but are not regular in the sense of being a major nutritional resource (e.g., Watts and Mitani 2002; Stanford et al. 1994). q19

To me, the relative unimportance of meat to chimpanzee diet is one of the significant differences between chimpanzee meat eating and early hominin meat eating. Others are that chimpanzees (1) use many tools but rarely use them for acquiring animal foods (Stanford 1996; Whiten et al. 1999), (2) take only small animals as prey (e.g., Boesch and Boesch-Achermann 2000; Mitani and Watts 2001; Pruetz and Bertolani 2007), and (3) rarely scavenge from carcasses killed by large carnivores (Watts 2008) and so do not risk death or injury in direct interference competition.

If prelithic hominins behaved like chimpanzees (though chimpanzees are not necessarily a good model for prelithic hominins), then it is a matter of opinion whether they did or did not possess "the obligatory ultimate and proximate motivations, as well as the physical capabilities, for regular acquisition and eating of meat" as Pickering suggests. I would say that modern chimpanzees have these abilities but do not often exercise them in the wild—which could be said, also, of the stone-tool-making abilities of bonobos (Savage-Rumbaugh and Lewin 1994; Schick et al. 1995; Toth et al. 1993). Pickering might say that chimpanzees have such abilities and so their possession is not unique to humans. I am reluctant to draw firm conclusions based on analogies to a modern species that has had 6–7 m.yr. of evolution since their lineage diverged from ours in which to change their abilities and behaviors.

Finally, Klein observes that something changed dramatically in human behavior and evolution about 50,000 years ago. He remarks that the animal connection may have started 2.6 mya but that the most obvious effects of have occurred mostly after about 12,000 years ago.

I take this to mean that he does not feel entering the predatory guild at the time of the invention of stone tools was highly significant. Here I and others disagree with him (see Blumenschine and Pobiner 2006; Bunn 2006; Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003; q20 Shipman and Walker 1989). Ecologically, making a transition from a largely herbivorous or even omnivorous niche to a predatory one is of tremendous importance. There are few examples in the mammalian world of species that have made such a transition, perhaps because it has such momentous consequences.

Klein argues that "whatever enhanced human fitness about 50,000 years ago also explains those aspects of the animal connection that are truly unique." In another publication, Klein (2000) has suggested that the enhancement was caused by the invention of language. I certainly agree that the origin of language was a formidable "enhancement mechanism" in human evolution. I argue that its roots can be traced to the growing importance and volume of information about animals, which is the predominant topic recorded in the first symbolic communications (prehistoric art) that we can decode. As yet, we cannot decode the earliest symbolic behaviors of humans, such as the geometric designs engraved on ochre pieces at Blombos Cave some 77,000 years ago (Henshilwood et al. 2002). If we become able to identify the meaning of those symbols and if they refer to information about animals, this will strongly support my idea that the need to store and communicate information about animals spurred the evolution of symbolic language.

An increase in population density as humans moved into Eurasia may also have played a vital role in the origin of language. Having a community of people with whom to communicate—who share the same symbolic vocabulary—is an essential component of the development of language. Alas, in areas of low population density, incipient language may fall not on deaf ears but on no ears at all. I appreciate the suggestions, criticisms, and ideas my colleagues have offered in response to my animal connection hypothesis and look forward to many more lively discussions on the topic.

—Pat Shipman

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QUERIES TO THE AUTHOR

q1. OK to change Bickerton 2000 to 2009 to match references cited?

q2. Which Childe reference were you citing with "Chidle's hypothesis"? We would prefer to restate if necessary or move citations if possible. Please advise.

q3. In the block quote from Clutton-Brock, do the same reference and page numbers apply as from the previous sentence?

q4. In the sentence beginnig "Rarely," there seems to be a word missing. Did you mean "children are seen as feral dogs" or "with feral dogs"? Please revise as necessary.

q5. OK to say "at about 12,000-10,000 B.C.," or should it be "12,000-10,000 years ago"?

q6. OK to change Tishkoff et al. 2006 to 2007 to match references cited?

q7. In the future, please be sure to include full inclusive page numbers for each reference. Many of the final page numbers were missing, and I researched the references and supplied them. Please check throughout and verify accuracy.

q8. For American Association of Pet Product Manufacturers 2007, if possible, please provide title of survey and location of the association.

q9. For Australian Companion Animal Council 2006, please provide location of association.

q10. For Fenson et al. 1994, please provide inclusive page numbers.

q11. For Flannery 1973, did I provide the correct full reference information?

q12. For Harris Poll 2007, please provide location of Harris Poll.

q13. For Headey et al. 2003, please provide inclusive page numbers if possible.

q14. For Headey et al. 1999, please provide inclusive page numbers if possible.

q15. For Izar et al. 2006, please provide inclusive page numbers.

q16. For Nature Australia 2002, is this a newspaper? Can you provide a section or any further information?

q17. For Pet Food Manufacturer's Association, please provide location of association.

q18. Sablin and Kholpachev 2002 is not listed in the references cited.

q19. Watts and Mitani 2002 and Stanford et al. 1994 are not listed in the references cited.

q20. OK to change Dominguez-Rodrigo 2001 to 2002 to match references cited?