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the Evolution of Culture

Duane Quiatt and Vernon Reynolds

Excerpt

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1 *Introduction*

Our objective in writing this book is to examine the theories and evidence that bear on the subject of primate social evolution. We draw on the efforts of a generation of field workers, and on theoretical analyses concerned with the organization and evolution of social behaviour in the order Primates. Where necessary, we also draw on laboratory studies. We write as *anthropologists* and so we are concerned with the emergence of human cultural social organization, and we attempt an elucidation of the critical path which has enabled this to happen. Our approach lays emphasis on the cognitive nature of primate social communication, the need to understand primate social interactions as founded on the transmission of information, and the role of language in enabling the formulation of new levels of complexity in social formations in humans. The entire analysis is grounded in neo-Darwinian evolutionary theory, with especial emphasis on the utility of a socioecological approach, and we use this approach in an attempt to understand the emergence of human kinship systems, arguably the backbone of human social organization.

Primates live in the real world, the world of trees and rivers, rather than in some theoretical hyperspace. In this real world that they inhabit, the extent of interference of human beings varies from great, as in the case of groups of monkeys, in, say, a Japanese monkey park or around a temple in India, to small, as in the case of field studies conducted in undisturbed rain forest. Field studies present a range of interferences: the intrusion of the observer on the behaviour of the animals, seen most clearly for instance in studies relying on 'provisionization' (feeding) for access to the animals. Besides these 'real' interferences, there are further distortions resulting from the use of human language to describe what primates do, and behind these lurks the theoretical perspective determining the observer's interpretation of what is seen, which again introduces a selectivity. We need to be aware of these biases, but not allow them to defeat the object of our enquiries. Despite them, we can draw meaningful

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conclusions from primate studies, distinguish between varieties of ecosystems and of social organizations in those ecosystems, and draw out a way of understanding human social evolution.

Behaviour, including social behaviour, is characterized by variability, and this variability is the material on which selection works during evolution. There are two sources of variability in primate social behaviour and social organization. (By social behaviour we mean the ways in which animals interact with one another; by social organization we refer to the network of relationships making up the structure of the group as a whole.) The first is the product of what can be called ultimate causes and is the outcome of selection at the genetic level. The second is the product of what can be called proximate constraints and is the outcome of interaction between individuals and their socioecological circumstances. Both sources of variability are inextricably intertwined in actual life, but are analytically distinct. The result of the variability is that some individuals achieve greater individual fitness than others, and if we include the effects of their behaviour on their kin, then some individuals achieve greater inclusive fitness than others.

Primate habitats are largely arboreal, but a number of primate species have succeeded well in adapting to terrestrial habitats, and it is in such circumstances that some of the more complex forms of social organization have emerged, such as the matriline-based systems of some macaque and baboon species. Pressures that have led to the evolution of such systems include the presence of predator and prey species, and the richness and distribution of food supplies. Habitat diversity has led to different solutions to the problems of finding enough food in different primate species, and we find differing ways of ordering the relations between groups and the space they occupy according not only to the distribution of preferred foods but also to seasonal factors and the presence of other groups nearby. As a result, we find primates organized into multi-male groups, one-male groups, monogamous groups, or complex fission–fusion groups, presenting us with a challenge of explanation.

Behavioural ecology, which can be broken down into sociobiology and socioecology, has largely transformed our understanding of the part played by individuals in social evolution. Let us first consider the long-term or ultimate causes underlying social behaviour. For many years there was a debate between those who favoured group selection in the explanation of social organization, and those who favoured selection at the level of the individual. (By ‘group selection’ we mean the idea that it is groups that compete with each other for survival during evolution; the

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behaviour of individuals within groups is in the interests of the group as a whole (i.e. not just in their own interests), and so the best adapted groups pass on their genes while those that are less well adapted die out. By 'individual selection' we mean that individuals compete with each other for survival during evolution, and the fittest (in the Darwinian sense: i.e. those that achieve most reproductive success) pass on most genes to the next generation, while those that are less fit pass on fewer or no genes. Groups exist and survive because it is in the survival and reproductive interests of the individuals in those groups to live together and make compromises rather than living alone.) That debate is now largely over in respect of all animal species other than human beings, the latter view having superceded the former. Explanations of social cooperation and even altruism can be derived from a basis of individual competitiveness and selfishness. The twin processes of kin and reciprocal altruism, introduced by Hamilton (1964) and Trivers (1971) respectively, have been shown to have considerable explanatory power in explaining long-lasting, kin-related groups such as those characteristic of primate species.

There remains much to be incorporated into this perspective, however. For example, the distribution of genes in populations studied by population geneticists has yet to be properly integrated with behavioural ecology, and the differential fitness of individuals in groups has yet to be integrated with patterns of gene flow across generations.

Studies of primate social behaviour at the present time focus on the nature of dyadic interactions, of competition and cooperation between individuals, of the results of these on the social organization of groups, and of how individuals in social groups come to adopt particular strategies for mating and obtaining food. In the understanding of these matters, it has become clear that primate behaviour is the outcome of a continual learning process in which individuals constantly make adjustments to other group members. An economic model, viewing behaviour in terms of costs and benefits, has proved rewarding in making it possible to tie up observed behavioural outcomes with expectations derived from sociobiological and socioecological principles. Field studies have been especially productive in yielding successful analyses, but studies in captive settings where more environmental and social factors can be brought under control are essential in deciding between rival explanations.

How can strategies of the genes be connected up with the observed actions of individuals in social settings? No simple answer has been found, or is likely to be. The problem is the pervasiveness of compe-

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tion, which means that any successful strategy will eventually give rise to a rival strategy, to which it will have to respond or perish, and so on. There is thus no way in which a simple set of rules of thumb can deal with each and every situation in an intelligent species such as a primate. Instead, what seems to have evolved is a set of condition/action rules for behaviour, i.e. rules that specify action according to circumstances. Strategies, consisting of a variety of tactics, comprise nested sets, giving behaviour a great variability. In order to make sense of social behaviour and organization, we have to discover regularities, and the first priority is an effective method of description. This has to some extent been achieved by the separation into levels of interactions, relationships, and social organization (Hinde 1976). (The distinctions are as follows: interactions are the patterns of behaviour that are seen when individuals are in interaction with each other; relationships are kinds of long-term associations between individuals; and social structure is the network of relationships constituting the group as a whole.)

The question remains, however, of the nature of the communicative process within the relationships in this scheme. The traditional ethological view of communication as the transfer of information has more recently been challenged by the view that communication is essentially manipulative (Dawkins & Krebs 1978). While there is some truth in the latter view, it is not conducive to an understanding of much of the communicative process in primate society. Primates have been shown to communicate quite sophisticated information to each other about individual identity, food sources, and kinds of predators. This is perhaps because primate behaviour is cognitively organized, and also because groups are mostly based on kin (normally female, but occasionally male), between whom the benefits of communicating information outweigh the benefits of trying to manipulate one another for personal gain. Also, from the anthropological perspective of trying to explain the emergence of human social organization, an informational approach seems particularly useful.

Simulations by computer programmers of information processing in the field of artificial intelligence (AI) have led to the emergence of quite sophisticated and lifelike mechanisms, such as chunking by which Allen Newell's Soar system learns from experience, converting goal-based problem solutions into long-term memory productions (Newell 1990). Solutions to problems, once solved by the program, are short-cut next time the same problem is encountered. Primates in social groups have to solve problems all the time, and may learn by such methods. What they learn is information about the other members of the group, and their

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fitness is determined by the use they make of this information. The idea of an information-based patterning of social knowledge provides a basis from which to explore the evolution of the institutions of human society.

How do primates 'see', or comprehend their environments, physical and social? Like all animals, they experience the world outside through their senses, mainly vision but additionally hearing, smell and taste. For vision and hearing, monkeys, apes and humans appear to have a lot in common. In our own species, we know from psychological studies that we perceive the world around us very selectively. Of the constant bombardment of our senses by the outside world, our brains and minds select what is relevant and form coherent pictures for us. Perception, for all species, is the interpretation of sensations, making sense of what is apprehended by the sense organs, and linking this up with knowledge stored in memory.

Experimental work has shown that primates are capable of transfer of learned information across sensory modalities, e.g. from the visual to the auditory, and that this ability is greater in apes than in monkeys. Here we may perhaps find clues to the evolution of spoken from gestural language.

Social perception is well developed in primates, and they have been shown experimentally to be capable of distinguishing their own relatives from unrelated group members. This knowledge about relationships can be included in the general category of social cognition. The complexity of primates' abilities to make social distinctions is paralleled in their demonstrated mental agility in experimental tests conducted by psychologists. For example Weigl oddity tests have shown that primates have the ability to generalize and so solve novel tests on the basis of rules learned in a different setting. The fact that they have a longer latency on harder tests has been taken to indicate the occurrence of vicarious mental calculations. Experimental demonstrations of the ability of primates to rank objects in a hierarchical order indicate that in a social setting this ability will be available for the organization of social relations.

These clues about primate cognitive capacities, derived from very contrived and controlled experimental tests are of interest for present purposes because they demonstrate the cognitive underpinning of primate social life. In fact, underneath this life there lies a highly evolved intelligence capable, as we know from experimental work, of making complex predictions. The biological significance of social interactions hinges on the implications for fitness, fuller understanding of which requires that we put the cognitive social skills shown by primates into a sociobiological frame of reference.

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In social life, primates appear to act intentionally with regard to the strategies they pursue, but we need to beware of concluding that their kind of intentionality is closely similar to our own. Human cognitive psychology looks at the underlying biases, prejudices and presuppositions guiding social action, but this approach is not open to primatologists who must work from an assumption, namely that the behaviour of animals is fitness-oriented. Social cognition thus requires a broad definition that does not foreclose its functions, and we suggest 'the application of intelligence to review of social information and the exploitation and management of social relationships toward attainment of proximate goals' (See Chapter 6, p. 141 for further discussion of this topic.)

Social information derives from various sources including communication with other individuals. Playback experiments in the field have shown that vervet monkeys can distinguish different meanings from slight but regular acoustic differences in alarm calls. Further, they can distinguish home-group from other-group members, and dominant from subordinate group members, by vocalization alone. Thus, besides their expressive or affective function, primate calls are laden with rather specific meanings relevant to the precise situation in which they occur.

It has further been demonstrated that not only do monkeys recognize their own relationships with others, but they can recognize the relationships between other individuals in their social group. For instance, mother–daughter pairs can be matched even from photographs of the individuals concerned. Such abilities provide clues to the ease with which primates take sides in disputes between members of their own and other matriline.

Social knowledge can be defined as 'knowledge concerning the identity of conspecific others, the character of their behaviour as individuals, and the specific nature of their relationships with one another, including oneself' (See Chapter 6, p. 148 for further discussion.) Much knowledge useful for survival can be acquired only in the social context, though it requires careful observation over long periods of time to discover how knowledge is derived from the social setting. Social knowledge, in chimpanzees at least, includes knowledge about the self, demonstrated by mirror image experiments. This ability to objectivize the self leads to a further elaboration of the complexity of social action, with the inclusion of self-awareness and self-monitoring during social interaction. The nurturing of grievances by chimpanzees, leading to aggressive revenge at long time intervals from the causal events (de Waal 1989c) indicates a

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powerful sense of self and, in the context of kin alliances, allows us to link up with the human institution of the feud.

Do interactions in primate social life really need such complicated explanations? Are they not capable of being fully understood in terms of stimulus–response sequences? There is no doubt that they could be so described: any behaviour can. What is missing from such oversimplified description is the background of information review and processing that leads primates to decisions such as *when* to try for a takeover, or *whether or not* to make a sexual advance to a potential partner. Do primates ‘have intentionality’? What does that mean? By the analysis of cases of what appears to be deception, Whiten & Byrne (1988a,b) have shown that primates act *as if* they were working with a high degree of intentionality. As Kummer *et al.* (1990) have pointed out, further work of a more experimental kind may shed more light on such cases.

The peculiarly difficult problems presented by the analysis of deception in primate social interactions confirm that it is impossible to prove, in natural situations, that an animal intends or intended to deceive. Our own view is that primate social action is controlled by a self-conscious intelligence which functions to contemplate alternative possible courses of action and decides on the one likely to yield the best pay-off. This view is based on our own fieldwork with primates and our trust in the interpretation of others of what they have observed. The evidence in this area is necessarily somewhat anecdotal and has been subject to considerable criticism on this count. Much of this criticism is methodological. Readers will be able to see from the examples of deception in Chapter 7 what some of the methodological problems are. One issue that emerges is how to interpret objectively sets of events by after-the-fact examination of the relationships between those events.

What, if anything, can be done to bring greater precision to this issue is a currently debated issue. One aid that can at the least render behavioural observations subject to re-analysis is the use of visual recording media. This can enable re-running of a sequence that might otherwise be a mere anecdote. Experimental manipulation of relevant variables in tightly controlled settings is probably the way forward, however. Studies of the contexts in which ever more subtle tactics of deception are learned is a further way towards clarification of the processes involved. The demonstration of deception is highly situation-dependent, another complicating factor. Regularities must be sought, and these appear to include the non-transmission of information, the inhibition of action, and the hiding of give-away clues.

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The significance of deception is that it involves, in primates, the manipulation of social information, or what we have called 'knowledge in the social domain'. Not all such knowledge is manipulated, indeed for the most part it is shared, so that it comes to form the body of social knowledge the animals in a group share with each other, and can communicate with each other about. The approach to the understanding of social life solely through the perspective of selfish individualism is a partial one; it omits emphasis on reciprocity, shared knowledge and the mechanisms by which relationships are maintained. It also misses the system aspect of society – the flow of information through the group that constitutes the dynamic of its socioecological adaptation.

Three *repositories* of socially communicable information can be distinguished: 1. individual memory, 2. the group's working knowledge, and 3. culturally stored knowledge – the extra-somatic archives characteristic of but not exclusive to human society. The latter for instance include the discarded sticks used for termiting by chimpanzees, which pass on technological information, or the anvil and stones used for nut-crushing by chimpanzees, which remain *in situ* for the use of others.

The second repository – the group's working knowledge – is less tangible than the third but no less real. It arises from activities performed by the group as a whole. In humans, we have the process of oral tradition of stories and songs, found all over the world. In non-human primates examples include the cooperation of all group members to locate good food sources, to deter predators by mobbing them, to escape from predators by sharing information about their species and whereabouts, or to solve problems. The latter is especially clearly demonstrated in experiments in captive situations where, for instance, chimpanzees cooperate to hold a long, heavy branch to get over an obstacle between themselves and freedom or food.

The 'language' training, or training in symbolic communication of chimpanzees and other apes demonstrates one characteristic of social knowledge, namely the setting up of a rather narrowly defined domain of knowledge, a world in which certain things or hand movements, and they alone, constitute the information base. In this closely confined world, knowledge of significant features and relationships is acquired in the course of strongly affective interaction between an ape and his or her trainer, or, as in the case of Sue Savage-Rumbaugh's chimpanzee subjects, Sherman and Austin (Savage-Rumbaugh 1986), who have to communicate symbolically to solve problems, between ape and ape. Similar 'small worlds' have been simulated in computer representations

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of robotic activity, with a small number of variables set to interact with each other in semi-lifelike ways. Real life groups are more open, and the passage to humanity involves a progressive opening up of the world of communicable information.

The institutionalization of relationships involves conventionalizing of knowledge in the social domain. Language is not essential for this but presumably it is essential for the evolution of *human* society. With language, the world becomes a construction, to which knowledge of the language is the key. Without language, roles can nevertheless become differentiated in conventionalized ways, as for instance in the case of lid-lifters and non-lifters among Cayo Santiago rhesus monkeys. A surprising feature of such cases is the constancy with which roles are maintained over long time periods. The playing of roles by humans who are constrained by social and economic forces shows similar constancy. In the human case, language affords conventional names for concepts and relationships and thus enables the ramification of roles in social life. Advantages in evolution accrued to those who could implement systems of categorization of information, most particularly in the extensions and re-groupings of kin seen in kinship systems, and in the construction and implementation of marriage rules and systems of affinity.

Kinship is the most elementary of all human social structures, and was probably the first area of social life to be subject to conventionalization and categorization. In macaques, matriline exist as functional elements in the social structure, having a primary function in relation to status. Young animals are able to acquire a status consonant with that of their matriline by virtue of support from matriline members in disputes with members of other matrilines. The matrilines themselves are in competition with each other, and if, for any reason, a matriline is weakened, its members may be attacked by those of another matriline and status reversal may then take place.

The analysis of primate and human lineage structures is often achieved by means of kinship diagrams. The conventions used in these give clues to similarities and differences. An important similarity is the fact of biological (genetic) relatedness. All members of a primate matriline are so related. Human lineages are more complex, but they too are based on biological relatedness. We assume monkeys do not 'know' they are related to each other in the sense that we know that, but their relationships show different degrees of closeness or distance, and willingness to form alliances depends on the social psychology of relationships.

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In human families three processes are integrated into the psychology of relationships, first the linguistic environment, second the technological environment, third the socio-legal environment. While these are prominent in human social life, equivalents of all three processes can be found in non-human primate society. In particular, these processes depend on the transmission of information and its learning by subsequent generations. For example, it is knowledge of membership of matriline that enables monkeys to form appropriate alliances in inter-matriline conflicts.

Patrilines are unusual in primates, but do occur, for example in chimpanzees. The principles outlined above apply in the case of patrilines, except that father–son relationships replace mother–daughter ones. Patrilines and matriline are not the same as patrilineages and matrilineages, because they involve, in primates, members of one sex only, whereas in humans both sons and daughters are members of the patrilineage or matrilineage. In primates, the ‘line’ is a co-residential, face to face sub-group within the whole group, and which sex is involved depends on which sex forms the permanent core of the group and which one emigrates at puberty to find a mate elsewhere. In human societies, too, it is often the case that one sex or the other leaves home at marriage, but his or her lineage ties are maintained thereafter because of the greater persistence of lineality in the context of language-based culture.

Paternal behaviour in primates was once thought to be virtually non-existent, but is now known to exist in most species. Male care of infants is widespread, and in species living in multi-male groups such as baboons is most extensive in the case of males who have formed a lasting association with a female, where it tends to be focussed exclusively on the offspring of that female (and hence very likely of the male too). This indicates the general rule: males are concerned to promote the survival of their own (genetic) offspring. In polygynous primate species living in one-male groups,¹ such as Hanuman langurs, there is fierce inter-male competition for group leadership, associated with infanticide by takeover males as a method of ensuring paternity of the group’s infants. In monogamous species such as gibbons there is, by contrast, complete cooperation between males and females in territorial defence; this is associated, because of monogamy, with high paternity confidence.

The issue of paternity remains with us in modern society, as the issue of genetic techniques in legal paternity claims bears out. In most human societies, the father of a child has certain obligations towards that child’s mother and the child itself, though these obligations vary from one