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Mammalian Social Learning:

Comparative and Ecological Perspectives

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The myth of peculiar primates

Thelma Rowell

We are, today, a nested set of people interested in animals. The Zoological Society encompasses interest in 'all creatures great and small', the Mammal Society selects those with hair and milk, and the Primate Society confines itself to some 200 hairy, milky species, a single Order of a single Class of a single Phylum of animals. Why isn't the primate society a special interest section within the mammal society, of a size proportionate to the size of the order? Are Primates, and especially their social behaviour and learning ability, so different from other mammals? Is there really a valid entity called primatology, with its own methods, theories, and generalisations about its subject? Of course *we* are Primates, and there are an awful lot of *us* – but only a minuscule minority of people who study *us* would call themselves primatologists, so specific introspection is only a very minor part of the answer.

Logistical constraints on primate studies

The zoologists who began to study primate social behaviour in Europe were ethologists who had previously worked on the behaviour of birds or fish (not other mammals). Zoologists traditionally worked from type specimens: an animal represents its species, with some ordered variety due to sex, age and perhaps season. Beyond that, variation is a nuisance for a typologist. It can often be assumed to be the result of observational or experimental 'slop', and fortunately a nice large sample size allows statistics to tidy up such problems and reveal a 'true picture' – a mean or modal value. In a more modern approach, the variation in the sample becomes of interest in itself, and one might be interested in changes in variation as conditions change, or changes from generation to generation.

The new thing the early monkey watchers did, I think, was to recognise the individuality of their animals. Recognising individuality is not at all the same as recognising variation, which is a property of populations. I don't think we deliberately chose to recognise individuality – the step was forced on us because you never have enough primates to study in more traditional ways. They are extraordinarily expensive to keep in captivity, and in the wild they are

mostly on endangered species lists, mostly live in dense vegetation high over your head, and in small groups at that. And they live long lives, very slowly. All this means that each precious specimen is studied intensively and for long periods, and the differences between them become inescapable: instead of a sample of specimens you have series of individuals, each with a history: a series of experiences which *cannot* be the same as those of any other animal, as well, of course, as a genome which is unlikely to be identical with any other.

For years we monkey-watchers have mostly seen this as a problem and tried to ignore it: we clandestinely enjoyed the unfolding soap operas in our monkey groups while striving to extract and present generalisations to our colleagues. Biology must surely be more than an endless series of individual biographies, and while individuals are not identical, they do have *similar* histories and *similar* genomes, so on the whole we played down the individuality and stressed the similarities. Nonetheless, studying individuals does provide different opportunities, as well as imposing some serious limitations, on research.

These are not concerns I detected as I started reading about the behaviour of sheep, which are also largish, longish-lived, and highly social mammals, and I began to wonder why. I can think of three possible reasons.

1 Perhaps because of the logistical reasons I have outlined, questions asked of sheep and monkeys have been different. More sheep are available and they turn over more rapidly so you can do more controlled experiments of short duration, and in the wild you can be concerned, practically, with population dynamics. The question of individuality hasn't arisen.
2 Perhaps the people are different: people who don't like soap operas don't do long-term studies of monkeys.
3 Perhaps the animals are different: sheep, and other nonprimates, might actually show less individuality than any primate.

Since the first two reasons are surely valid, we haven't adequate evidence to accept or reject the third yet, and I will come back to it later.

The people who study primates

Most zoologists find more productive subjects than primates – given the glorious diversity of animals, it is usually possible to find a more accessible and numerous subject group with which to answer almost any question in zoology. Most people who study primate behaviour have backgrounds in the social sciences, and in the US almost all of them are based in anthropology departments. This is mostly due, I think to the genius of one man, Sherwood

Washburn, an anthropologist at Berkeley, who in the early 1960s managed to parlay the general interest in human origins and human past into *actual money* for studies of primate social behaviour in the field and laboratory (Washburn and deVore 1961).

The interest he exploited was based in LeGros Clark's (1959) idea, that living primates could be classified into a series of grades, or steps. This is a closer look at the last few rungs of the old *échelle des êtres*: one after another, a series of primate taxa evolved an increasing distance towards achieving humanity, and then somehow ran out of steam and stopped. Thus they present a series of vignettes of the stages leading towards the emergence of humans. All we need to do is to walk back down the steps to go back in time and understand the origin of humanity. I am not imputing this simplistic view to Washburn himself, but I do think it is a fair caricature of the attitude he was able to exploit. It is an example of what I call the 'little furry people' approach to primates. People are too complicated, and often averse to being studied anyway. Other primates represent successively simpler versions of people, easier to analyse and available for experimentation. To an extent, they replace anthropology's lost hope of identifying primitive people to study. This interpretation is based on a completely outdated view of evolution and indeed of primate taxonomy: there is no evidence that any modern primates have stopped evolving, nor that they were striving to become people and can be seen to have failed in that endeavour to varying degrees, nor that differences between us and other primates can all be described as deficiencies in the latter (as in 'sub-human primates' – what a revealing phrase!).

Looking at primates because people are primates carries implications that need scrutiny. There is a clan pride which presumes that *our* relations are *better* – even quite distant ones. We might concede that elephants are brawnier, dolphins more agile, and both can hear things we cannot, but we consider ourselves socially superior and better at learning. So from the start we expected to find cognitive ability and social sophistication in our relatives, at least in nascent form – *and we looked for them.* So, it is students of primates that ask questions like: 'can we detect evidence of Machiavellian intelligence here, even in rudimentary form?', while a biologist trained in the reductionist paradigm would perhaps be asking of the same observations 'what are the minimal neural connections that would be necessary for this response pattern?'.

If you ask a stupid question, you get a stupid answer. If you phrase your question (that is, design your experiment or structure your observations) so as to be able to receive only a very simple answer, you will only get a very simple answer, even though it is only a part of the complete, complicated answer. There is also the danger of using entirely the wrong language when asking your

question. If we ask our animals questions in an irrelevant framework, we may get an answer which can be interpreted in that framework but is still actually nonsense. Everyone here would agree that an anthropomorphic framework could be irrelevant. How many would be prepared to consider the possibility that an evolutionary framework might be irrelevant?

Fools step in where angels fear to tread. In the West, zoologists learned from social scientists to ask questions of primates that had not been asked of animals before, and perhaps we taught them how to ask the questions properly. Japanese scientists, with the advantage of their own indigenous monkeys on the doorstep to study, and traditional knowledge of monkeys from which to start, expanded primate studies rather earlier. A Buddhist/Shintoist philosophical background leads to a very different approach to animal behaviour from the Judaeo-Christian one (and I hope the reader is not under the impression that their studies of animal behaviour are uninfluenced by their own cultural background . . .). Without the sharp distinction which is drawn between humans and animals in Western culture, evolutionary theory was not so revelatory in Japan – it didn't challenge fundamental attitudes, so it was readily acceptable – pretty ho-hum, really (Asquith 1986, 1991).

Also, there is a strong Japanese interest in the functioning of small groups. Studies in Japan began with parallel studies of many groups of Japanese macaques, and they recognised differences in behaviour between groups within the same population of monkeys very early. This led them to consider the possibility of 'proto-culture' among monkeys (Itani 1958, Kawai 1965a,b) with similar properties to human cultures – and that put them far ahead of Western typologists in the study of social learning.

My understanding is that on the one hand there is intense Western interest in the individual (at least in its fitness) and how it is affected by its relations with others. On the other hand, the Japanese interest has been primarily in relationships, and how they are affected by the individual. It was inevitable that at first Japanese and Westerners had a lot of difficulty in understanding each other (apart from Western linguistic laziness) as each side appeared to be taking for granted what the other was excited about. Both have gained from the effort to develop a common language. From the Western side, I think the Japanese approach has lead Westerners to appreciate higher levels of social complexity in primates than we would have otherwise reached by now.

'The further out from England, the nearer is to France' as the whiting pointed out (Carroll 1865). Did we inevitably widen the gap between monkey-watchers and other students of animal behaviour as we reduced the gaps between zoologist and social scientist, between East and West?

To summarise, I am suggesting that, first, we were from the beginning

forced to study primates in a different way because they are few and have slow life histories. We developed, and formalised, ways of handling the constrained data we could collect, methods which are equally applicable to other animals. Second, different and diverse expectations of and interests in primates have led to different questions being asked of them. These circumstances combined have been sufficient to give rise to a perception that primates are different from other mammals and so to extensive discussion of *why* they are different – and specifically, why they are cleverer and socially more sophisticated – rather like us.

Are primates different?

Much of the discussion about the peculiarity of primates has focussed on brain size and metabolic requirements of brains, and slow rates of development, and the possible adaptive significance of each and how they lead to each other (Pagel and Harvey 1993). It seems to me an argument which can be picked up at any point and carried on round in dizzying circularity.

From fieldworkers came suggestions of ecological factors: primates have a peculiarly varied and challenging diet to select, or a peculiarly complicated habitat to move through, or a special need for social sophistication, perhaps to enhance social learning. Any or all of these have provided a unique selection pressure on primates. Such discussions are generally written and read by primatologists, and have a lack of comparative depth. You are left asking, cleverer *in what way*, than what? a diet more diverse than whose?

There is a serious lack of comparative data, because people with nonprimate expertise have generally not asked the same questions. People who study elephants or dolphins simply do not accept the original premise of primate superiority; people who study rodents perhaps do accept it and simply draw the line which has always separated off people from other animals a little further out, taxonomically speaking, and ignored all primates – 'too difficult'.

Of course, primates are by no means the only mammals which are long-lived, difficult to observe, and available in small numbers. It is appropriate to treat all mammals to the pattern of intensive and sustained study of identified individuals as they pass through successive life-stages which has from the first characterised primate studies. Methods developed to deal with long-term primate observations are being applied to other animals, and we are at last getting comparable studies of group-living nonprimate mammals. We are hearing from some of the most exciting in this volume.

The descriptions coming in from all these studies have a basic ingredient in

common with the average primate social behaviour study – they all include patterns of interaction which are explicable, not in the present assessment of individual qualities, but *only in terms of past social events.* This is what is necessary in order to recognise evidence of long-term relationships between individuals in practice (Rowell and Rowell 1993). This, I think, is the basic ingredient in what I am calling 'social sophistication'.

It surprised a lot of people, both primatologists and other mammalogists, who expected only primates to be socially sophisticated. It was in 1984, at the International Congress of Primatology in Nairobi, that Lawrence Frank presented an account of his study of spotted hyena's social organisation entitled 'Are hyenas primates?', and thus perhaps opened the question to debate (Frank 1986; his paper was not included in the proceedings volumes of that congress). The point was that hyenas lived in an ordered society with many of the characteristics, the rules of conduct, which have been described for macaques. That was early days, and the point could be made even more forcefully now with the continued studies of the same population of hyenas by Holekamp and Smale (1993).

From that and a growing number of other studies, I do not gain the impression that there is an obvious break in the quality of social behaviour between primates and other mammals. It is also clear that there are no agreed measures or even definitions of 'social sophistication'. If this is an interesting question, we need criteria for comparing and rating social systems which are not constrained by the features of one order or another. That will need dialogue between primatologists and everyone else. Marina Cords recently suggested to me (in litt) that methods of conflict resolution might provide key criteria. I think social learning might offer another set of standards.

I suggest we start by abandoning generalisation about primates. This is an extraordinarily diverse order for its size, and I simply do not expect useful generalisations about social behaviour that cover gorillas and tarsiers and exclude nonprimates, any more than there are equivalent generalisations about their diet, or locomotion. For example, the small carnivorous nocturnal primates, such as tarsiers (*Tarsius* spp.) or Demidoff's bushbaby (*Galago demidovii*), can surely be more usefully compared with their niche-equivalents than linked, in generalisations about primate behaviour, with large gregarious diurnal folivorous monkeys such as howlers (*Alouatta* spp.). We know a little about their social organisation only because, as primates, they were assumed from the start to *have* social organisation. In contrast, rodents of similar size, although far better studied, were for a long time taken to have only fluctuating population densities.

In fact, most popular generalisations about primate social behaviour are

based on . . . most studies of primates, which have been of only a very few species. These are all species which spend much of the time on the ground and in fairly open spaces, and live in large cohesive groups, in which there is a lot of noisy squabbling and obvious makings-up. They give a high rate of return for observational effort, but they make up barely 5% of an order noted for its diversity of social behaviour, and of everything else.

We know by far the most about two to three species, each of just two genera – the macaques (*Macaca*) and the baboons (*Papio*). Chimpanzees (*Pan*) have attracted a lot of interest as our very closest relatives. The few other well-studied species are those most like the baboons and macaques within their own genera. Thus, among the African guenons we know most about the vervet (*Cercopithecus aethiops*) of open gallery forest and holiday resorts, rather than the 20-odd other *Cercopithecus* species which live quietly in dense forest. Similarly, the well-studied hanuman langur (*Presbytis entellus*) of Indian towns and temples is very different from the other 20-odd langur species which lead quietly boring lives high in the forests of southeast Asia. This handful of noisy extroverts, which is not taxonomically defined, consists of very peculiar animals indeed, not only among primates, but among all mammals. I marvel at their very existence, and I wonder why, and how.

I study guenons – blue monkeys (*Cercopithecus mitis*), in the Kakamega forest in Kenya, and occasionally baboon groups invade the area, looking for figs. My guenons and I hear them coming half a kilometre away. They are always squabbling among themselves, with screams and threat barks and grunts, and the moans of temporarily lost infants. My guenons make quiet alarm growls and freeze in creeper tangles, because baboons eat monkeys as well as figs, if they can get them. But surely baboons themselves are edible; certainly the local farmers are their sworn enemies, because they are effective crop thieves. How do they afford to devote so much time and concentration to interactions with other members of the group? I imagine my feral sheep allowing themselves to be so pre-occupied with intra-group squabbles, and the thought experiment produces instant mutton. Sheep would surely be wiped out by predators taking them by surprise while so distracted. Exploiting distraction in potential prey is a main tactic of predators: the sport of hawking with dogs relies on it, and in the suburbs cats make a killing at courting groups of sparrows in early spring.

The rate of overt social exchange within a forest guenon group is at least an order of magnitude less than in a baboon group. It is very quiet and peaceful, not to say a little boring, to follow a forest guenon group. Not much different, I find, from watching sheep, or deer. However, each group of related female guenons owns a territory, and nearly everything they eat grows within the

territorial boundary. Nearly every day they defend their boundary against neighbouring groups of females (the males dont seem to take part, but that is another story). These inter-group encounters are noisy and energetic affairs, typically lasting a quarter of an hour or so, but during them the two groups make as much racket as a baboon group makes most of the time. Eagles, which are the main predator of forest monkeys, sometimes make an attack during an encounter: the eagles apparently recognise that such intense social interaction is a distraction of which advantage can be taken. So when these quietly inconspicuous monkeys begin to behave rather like their squabbling relatives, they do seem to increase their risk. This must count as a major cost of group territoriality.

The functions and functioning of groups

In concentrating on the entertaining baboons and other squabbling primates, we have also concentrated on the pattern of interaction within groups, and the supposed enhanced fitness of those who successfully compete for status within a group. We have unravelled the making of alliances and counter-alliances within groups. All this obvious, entertaining social manoeuvring and manipulation is so laughably similar to what we see ourselves do, it must be a higher level of sociality than that of other, more discrete primates and other mammals – mustn't it? It needs to be demonstrated that we are dealing with substance rather than style here. The key question might be whether the interspecific differences in style of within-group behaviour translate into substantial differences between behaviour of groups. The behaviour of the group is an emergent property of that of its members, with qualities which cannot be described at the lower level of individual relationships. It deserves study in its own right (Hinde 1983, Allen and Starr 1982). The explanation for the behaviour of the few squabbling primate species could lie in the resultant differences in the behaviour of their groups. It is difficult to assess this possibility because of the extremely long lifespan of groups, which far exceeds that of the individual.

I believe that the primary function of groups was, and still is, protection from predators, and for brevity I shall confine myself to that aspect of group life. There are several possible mechanisms for this, but they are all more effective the better the members of a group coordinate their behaviour.

Patas monkeys (*Cercopithecus* (*Erythrocebus*) *patas*) first drew our attention to this (Rowell and Olson 1983). They are long-legged guenons which live cryptically in very patchy open woodland. Though they have long legs for a

monkey, they can't run as fast as dogs, so their only protection is first avoiding detection, and second, early warning and a sprint for the trees. Patas monkeys continuously scan their environment, moving their heads from side to side like little radar monitors, often standing on their hind legs to see over long grass. They watch for predators and they watch each other, and if they see anything suspicious they stop scanning and stare. The scanning neighbours instantly see the fixed stare and look the same way themselves. Thus, the presence of the possible danger is instantly communicated to the entire group, without anyone saying anything or making any flashy signal. Even during play or courtship the action is frequently broken off while both monkeys scan. The system only works if no-one is distracted. It is the perfectly cooperative mutual benefit system, not open to cheating. A monkey which did not play its part and keep scanning would only put itself at greater risk. It is a widespread system – once demonstrated so obviously by the patas, I could see it in other monkeys, and in sheep and in goats as well.

If guenons, and most other gregarious primates and nonprimates, keep distracting interactions to a minimum, baboons and the other noisy primates make a dramatic contrast which sets them apart. I ask again – how do they get away with it? They must either be unusually successful at evading predators, or for some reason be under very little threat from them. Or, they must gain some greater advantage from putting themselves at increased risk of predation. Are there comparably introverted nonprimates?

Once a group exists, it is going to function as an educational establishment. Even if you can imagine a gregarious animal with no interest at all in what fellow group members are doing, simply staying in the group as it moves around is going to mean acquiring the same home range and knowledge of local resources.

In the matter of predation, we see infant monkeys learning what not to be frightened of. When we arrive at our field site each year, a new crop of infants has been born, which react with alarm chirps when they first see us. Adults respond to their chirps by looking down at us, then return to their foraging or grooming. In effect they are saying 'Oh, that's all right dear, that's just Thelma' – and the infants never chirp at us again, indeed they come closer than the adults ever would.

Without pondering the exact mechanisms by which information is transferred between generations, then, a permanent social group accumulates local knowledge and, more interestingly, locally distinctive solutions to general problems, so developing the differences between groups which Japanese workers first described in macaques and called 'protocultural'. Are such differences confined to primates, or to some subset of primates? Has anyone

asked the question of nonprimates?

Groups are only parts of populations, which also include individuals which live outside groups, often for much of their lives. Groups interact with each other both directly, as at territorial boundaries, and indirectly through the migrations of individuals between groups. If we can watch for long enough, we see that some groups do better than others, thriving and budding off new groups, while others dwindle, and sometimes their remnants get absorbed by neighbouring groups. There is a large element of luck, no doubt, in the relative success of groups. None the less, what we are actually looking at is the differential survival of groups. The phenomenon really ought to be called group selection, if the term had not been commandeered, and much derided, elsewhere.

The problem, of course, is in the definitions. The population geneticist uses the word group to mean a breeding unit, a deme. I am using it to mean a social entity. In the very beginning, long ago, we used to assume that the social entity was indeed a closed breeding unit, before we understood about male migrations and other systems seemingly designed to limit inbreeding. With closer observation, and paternity testing, it becomes increasingly clear that the social system is not necessarily, even usually, the mating system. Somehow we still accept the limitations inherent in the population geneticist's definition and meekly ignore differences in success between social groups, concentrating instead on looking for differences between individual's relative success within a group.

If selection can act on the behaviour of groups, it is acting on the result of social learning within groups. What is being selected is the ability of the individual members to engage in the transmission of information, and their ability to cooperate with others in mutually beneficial activities like predator detection.

My next question is whether the *style* of interaction within groups might enhance the environment for social learning – or otherwise. It might just be that the squabbling primates have severally invented a better system of within-group education.

But that is quite enough speculation.

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