THE NATURE AND EVOLUTION OF BEHAVIOURAL NEEDS IN MAMMALS

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Abstract

Mammals are unique among vertebrates in experiencing a need to carry out behaviours which are not necessary for their immediate survival. This poses questions as to the nature of these behavioural needs, how they evolved and their implications for the welfare of mammals in captivity. Evidence is provided to show that mammals carry out daily programmes of activity which meet four kinds of requirement, namely, for security, appropriate environmental complexity, novelty and opportunities for achievement. Within their programmes mammals perform two kinds of activity: work, which relates to day to day survival, and leisure, in the form of curiosity or play, which provides experience which may prove to be of value in the long term .

The existence of behavioural needs is consistent with our knowledge of mammalian evolution. Even the earliest known mammals, living over 120 million years ago, differed from reptiles in having brain to body size ratios four to five times greater. The increase in brain size resulted largely from the massive expansion of a region of the cerebral cortex, known as the neopallium, which acts as a co-ordinating centre for sensory data, and creates a model of the world which determines subsequent action. During the 60 million year tertiary era, relative brain size increased in most orders of eutherian mammals, so that only the more intelligent survived.

Because mammals rely for their survival on collecting and analyzing data and acting intelligently, they need facilities to search for information to establish and monitor their concept of the real world; their psychological well-being depends on an environment which offers such facilities. There are two kinds of behavioural needs; psychological needs, which appear to be unique to mammals, and ethological needs which are experienced by all vertebrates. It is concluded that environmental quality for captive mammals should not just be assessed negatively, by the absence of abnormal behaviours, but more positively by the extent to which it meets their psychological needs.

Keywords: *animal welfare, behavioural needs, evolution, intelligence, mammals, psychological well-being*

Animal welfare implications

Mammals have uniquely evolved psychological needs and their well-being depends on providing them with facilities for an appropriate, satisfying programme of activity.

Introduction

There is now a considerable literature on techniques for meeting the behavioural needs of captive farm animals and non-human primates. Interest has been further stimulated by the *European Convention for the Protection of Animals Kept for Farming Purposes* (Council of Europe 1979) which specifies that farm animals should be housed according to their 'ethological needs' and the 1985 amendment to the United States of America *Animal Welfare Act* (USDA 1991) which requires provision of adequate facilities to promote the psychological well-being of laboratory primates'.

Thus the behavioural needs of animals now have a legal reality and there is a great deal of evidence that they are an important biological phenomenon. However, behavioural needs are not restricted to laboratory primates and farm animals, their existence has been recognized in a whole range of mammalian species (Hediger 1955, Markowitz 1982, Shepherdson 1989, Stauffacher 1992). It seems reasonable therefore to assume that all mammals have behavioural needs.

This article seeks to define the behavioural needs of mammals, to show how the concept of behavioural needs fits in with current knowledge of mammalian evolutionary history and, finally, to consider the implications for mammalian welfare.

The existence of behavioural needs

All animals have to acquire food, adapt to climatic changes, avoid enemies and compete for living space. The ability to do these things meets their physiological needs which are essential for survival in nature. However it is possible to keep a mammal such as a monkey, bear or sea lion in captivity where, seemingly, all these essential needs are met and yet, under such circumstances, they often develop abnormal behaviours and show signs of distress and boredom (Wemelsfelder 1984). Needs are generally identified through deprivation and it is clear that many captive environments do not provide facilities for animals to meet their behavioural needs. The important word is *need* and Ewbank (1985) pointed out, that 'a need is not an option or luxury but a necessity'.

It has been found that environmental enrichment, which provides opportunities for the captive animal to work or play, will often reduce or eliminate symptoms of distress and that many mammals will actively work for goals when there is no physiological need to do so. For example, macaque monkeys will search through woodchip litter to find hidden food pellets even though they are available in a hopper in the cage (Chamove *et al* 1982). This seemingly inessential activity on the part of the animal seems, at first sight, to be in conflict with evolutionary theory, because it is wasteful of effort. It might be expected that natural selection would have eliminated any behaviour which squanders time and energy. Thus the concept of behavioural needs presents the biologist with an apparent anomaly; mammals seem to experience a need to carry out activities which are unnecessary for their survival.

A number of approaches have been employed to meet the behavioural needs of mammals. Experimental techniques which have proved most successful, have provided unpredictability in the environment, a facility to control meaningful parts of the environment (such as food availability) and finally, even for some relatively solitary species, direct physical contact with compatible members of the same species (Poole 1987). One of the problems facing those concerned with meeting the behavioural needs of mammals is the lack of a firm theoretical background from which these needs can be predicted and satisfied. At present, results are achieved by trial and error and success is judged by improvements in behaviour, such as reductions in frequencies of abnormal behaviour and an increase in complexity of their repertoires. Another approach which has proved successful is that of Dawkins (1990) who gave animals choices and made them work for an alternative option. This enabled her to assess the economic value of a particular choice by estimating how much the animal was prepared to pay to achieve it in terms of work or inconvenience, on the assumption that greater effort is a reflection of greater need.

It is a common belief that only a natural environment can fully meet behavioural needs. The evidence from research on environmental enrichment, however, shows that a complex, interesting artificial situation can often meet behavioural needs (Markowitz 1982). In addition, the wild situation may be hazardous and inhospitable for the individual. In the case of the naturally solitary orang utan there is evidence that in captivity, females and young males are very sociable. Poole (1987) suggested that the quality of social life of these apes can actually be better in captivity than in the wild. Some other solitary species such as polecats (*Mustela putorius*) may also opt to socialize in captivity and sleep in close proximity in the nesting area. In these solitary species foraging patterns in the wild preclude group living but clearly orang utans and polecats both have a propensity for it.

In captivity, chimpanzees will readily spend hours working at computer games and challenges (see Matsuzawa 1989). They cannot do this in the wild, but it certainly appears to meet some of their behavioural needs in captivity. Clearly, while a mammal's behavioural needs must be adapted to life in the wild, many species are sufficiently flexible to accept and enjoy substitutes.

Time budgets and programmes

Field workers studying mammals have been able to work out time budgets for them, which have shown that they carry out a daily routine of behaviour which involves activities such as checking or patrolling the home range, maintaining an exclusive territory or core area by boundary marking or vocal display, foraging, resting, nest construction, and, at certain periods of the year, seeking mates or performing parental behaviour. Their programmes in the wild are determined by the nature and complexity of the environment in which they live and the challenges which it creates in terms of hazards and resources. The way of life of the particular species of mammal also has a profound effect on its programme. For grazing animals, seeking food presents little challenge unless it becomes scarce, while species with diets which are either varied or require hunting skills will have more elaborate programmes for foraging. Large mammals, such as elephants, have little to fear from carnivores, apart from guarding their young, while small species, such as field mice are constantly vulnerable to predators.

In addition to behaviours directly related to survival or reproduction, mammals may take part in leisure activities such as play and the satisfaction of curiosity. From this we might conclude that all mammals have a relatively complex programme of daily activity and that behavioural needs are essentially a reflection of the desire of the individual to achieve this programme.

The difference between having a programme and simply doing things is that the individual experiences a need to fulfil its programme and will strive to achieve this goal. In contrast, simply being active would imply no aims on the animal's part. An example which is familiar to most people will suffice to illustrate this point. A dog which is taken for a walk at a particular time each day will regard this as part of its programme. If the owner decides not to take it for a walk and, for example, sits reading the paper, the animal will initially inform him that it is ready to go out, by crying or barking. If these signals are ignored, the dog will make physical contact in various ways, such as nudging the paper or sticking its head in the way, and in some instances even bringing its lead. This usually results in the reluctant owner responding to the dog's manipulation and taking it out. From this example we can conclude that the dog has a programme which it strives to carry out and that it adopts a variety of strategies to achieve it; there can be little doubt that the dog's behaviour is goal directed and that it knows what it is aiming for.

It is my contention that, through carrying out an appropriate programme, the mammal is able to meet its behavioural needs. We can regard psychological well-being as the state of mind of an animal which is able to carry out a programme which leaves it emotionally satisfied. The whole essence of a programme is that the animal strives to achieve a series of goals in an organized sequence, that it experiences a need to do so and becomes frustrated if it is prevented. However, if a particular series of activities within the programme cannot be implemented, mammals are sufficiently flexible to reorganize the sequence or adopt a different strategy to achieve their need.

In defining requirements, two considerations are essential; firstly, we must relate them to the animal's behaviour in its natural environment and secondly, determine whether a similar need can be identified in captive individuals. If an animal acts in a particular way in the wild, for example showing a fear of man, but does not do so in captivity, the absence of humans cannot be regarded as a requirement of its programme. I shall list what seem to be the four major requirements, for most mammals, in terms of what they demand from the environment, with examples of both how they apply in nature and in captivity.

The need for stability and security

Solitary mammals, such as mice, beavers, shrews, mink, leopards and bears, almost invariably have a fixed resting place or den to which they return during periods of inactivity. This place must be secure from predators and undisturbed by conspecifics.

Furthermore the area around this resting place will be well known to the animal and sufficiently safe to allow foraging and reproduction. Even the more mobile solitary species, such as orang utans make temporary bivouacs, but live within a familiar restricted area.

In captivity, the need for security can easily be met by providing nest material for rodents, drainpipes for ferrets or an enclosed den for a fox. An excellent example of a secure enclosure for a beaver is to be found at Drusillas Zoo in England, where the animals are provided with a lodge and facilities for building a dam (Williams 1990). For some species a high vantage point is important and both monkeys and leopards in captivity will choose to rest in elevated locations if they are available.

For mobile social mammals, such as troops of monkeys, security depends upon an arboreal habitat and also their intimate knowledge of terrain. For mammals with well organized societies, such as primates, elephants and dolphins, security also depends on living in a stable group of familiar individuals. For stability and security, these species need the companionship and affection of other individuals.

Appropriate complexity

Different species of mammal living in the same habitat show complex behavioural repertoires which utilize only some of the facilities available. This is true even for closely related species, for example, a mink and a polecat may live in underground burrows in the same woodland; both are small ground-living predators, but the mink swims underwater and fishes in rivers and even, on occasion, climbs trees, whereas the polecat is a purely terrestrial animal. It is quite possible to keep a polecat in an enclosure using a moat as a barrier. Thus, the two species, while anatomically similar, do not utilize the same features of the habitat, so that it would be pointless, for example to provide a swimming pool for a polecat, whereas it would be appropriate complexity for a mink.

We often see gorillas in zoos in grassy enclosures surrounded with a moat. To the human observer this seems much better than a cage with bars, however gorillas are forest animals, which do not live in fields so an open enclosure may be more impoverished than a well designed cage which can offer appropriate complexity in the form of a three dimensional habitat with facilities for climbing.

From studies in captivity we know that different mammals place a high priority on the facilities to carry out particular behaviours, such as rooting in pigs or branch gouging in marmosets. The provision of a substrate for the pig or branches for the marmoset therefore represent appropriate complexity. What is wrong with many captive situations is that they are too simple, but it is vital, when increasing complexity, to do so in such a way that it meets the animal's needs to carry out particular behavioural routines. It is not necessary to replicate an entire woodland for a squirrel in captivity but certain features, such as a soft substrate, nesting materials, a nest box and a climbing frame can be incorporated into enclosure design. Mammals do not just do one thing, so it is important to offer a variety of options for activity within the complexity of the enclosure.

An element of unpredictability

The natural environment may remain fundamentally stable but, from time to time, changes and unpredictable events occur. Exploratory behaviour, when a mammal patrols its home range, functions to detect significant changes and an important element of the animal's programme is concerned with the identification of novelty and change. The individual's survival and reproductive success depend upon the detection of environmental change. For example, a predator may have moved into the area; a rival extended its foraging range, or a potential reproductive partner set up home in the vicinity.

In captivity, mammals benefit from some novelty and unpredictability. New scents, sounds or objects, changes in topography, or access to a new area from the home base are all of interest; even simple changes such as providing fresh bedding will create novelty. Companions will also increase unpredictability because they change with age and experience. Many social interactions, including social play, have a dynamic component as well as a basic stability. However, an excess of novelty can be disturbing and counter-productive, for example removing a mammal from its home base and putting it into a new cage or enclosure can prove a very traumatic experience (Hediger 1955). Hence, we should only provide a restricted degree of unpredictability to the basically stable environment.

If captive mammals are deprived of novelty, some tend either to create it for themselves by, for example, destroying the enclosure, gnawing the furniture and so forth, or they may become hypersensitive to trivial stimuli. Other individuals, when they realise that nothing changes, simply become apathetic and bored.

Opportunities to achieve goals

In the wild, the mammal is presented with constant challenges in its search for food and mates and its efforts to avoid hazards. Failure will result in decreased fitness or even death. Mammals rely for their survival on using their skills to achieve goals, success is rewarding and pays off. Hunting species such as wolves and lions ambush or surround prey, more omnivorous species such as dwarf mongooses break eggs against rocks, chimpanzees fashion simple tools to probe for insects or make sponges from leaves to soak up water. In everyday life mammals rely on their skills and intelligence for survival.

In captivity, the satisfaction which mammals gain from achieving a goal is appreciated by anyone who has trained them. Animals as diverse as rats, walruses, elephants and chimpanzees gain satisfaction from achievement, quite apart from the actual food reward. The most intelligent species show clear evidence of pleasure in simply completing a task successfully. Working with an animal as a partner gives satisfaction to both trainer and trainee (Poole & Kastelein 1990, Pryor 1985, UFAW 1990).

The kinds of goal which can be provided in the laboratory are numerous, ranging from the most sophisticated computer game for chimpanzees to the simple puzzle which requires ingenuity to gain access to the food. In captivity, perhaps the most important way in which this requirement can be met is through training. European zoos are realizing, for example, that to keep psychologically healthy elephants in captivity, it is beneficial if they are trained to work. Highly intelligent mammals such as elephants, bears and primates may gain pleasure in achieving purely intellectual goals which have little to do with survival or physical needs.

Social life for some species may also provide opportunities for achievement. The individual may make a new friend, triumph over a rival, acquire sexual access to females or, in the case of chimpanzees, even achieve a 'political' end (de Waal 1982).

Companionship

The reason for not including a need for social companions among the four requirements of a programme is that many species of mammal are solitary and some even prefer privacy. Secondly, the four requirements differ from one species to another in the precise form they take. For group-living species, conspecifics supply the requirement for security (the troop or pack, individual companionship), relevant complexity (groomers, playmates, relatives, rivals), novelty (births, deaths, changes in social relationships) and, finally, opportunities for achievement (leadership contests, competition for mates, motherhood). For social species, other individuals therefore contribute towards meeting all four of the requirements of their programme and thus play a key role in their well-being.

The evolution of the mammalian brain

A most important question which has to be posed is whether we can accommodate the concept of behavioural needs in evolutionary theory.

Although the behavioural repertoire of fossil animals cannot be known with any degree of certainty, some aspects of the behaviour of extinct mammals and their reptilian ancestors can be deduced from their skeletal structure. Where the fossil record is adequate we can tell how they walked, and whether they were carnivores, omnivores or herbivores. Palaeontologists can also deduce from endocranial casts the relative volume of the brain in relation to body size; this can be converted into a ratio for brain weight: body-weight. In the case of mammals the endocranial cast closely follows the contours of the brain so that the external anatomy of the brains of fossils can be compared with those of living forms.

Mammals evolved from the Synapsida, mammal-like reptiles, approximately 200 million years ago in the late Triassic period. Anatomically advanced synapsids and primitive mammals were very similar (Olson 1971) but, as Jerison (1973) has emphasized, they differed in one most important respect. Even the most advanced synapsids had typical reptilian brains lying within the size range of all extinct and modern reptiles. In contrast, even the archaic fossil mammals had brains which were similar in form to those of modern mammals, but were four to five times larger than those of their close relatives, the contemporary synapsid reptiles. Figure 1 shows the ratios of brain to body size for reptiles and those for species of mammal occupying ecological niches which were exploited in the Mesozoic era, namely, insectivores, carnivores and rodent-like herbivores. The polygons show that all mammals had considerably larger brains than reptiles of equivalent size, but those living today have larger brains than their predecessors.

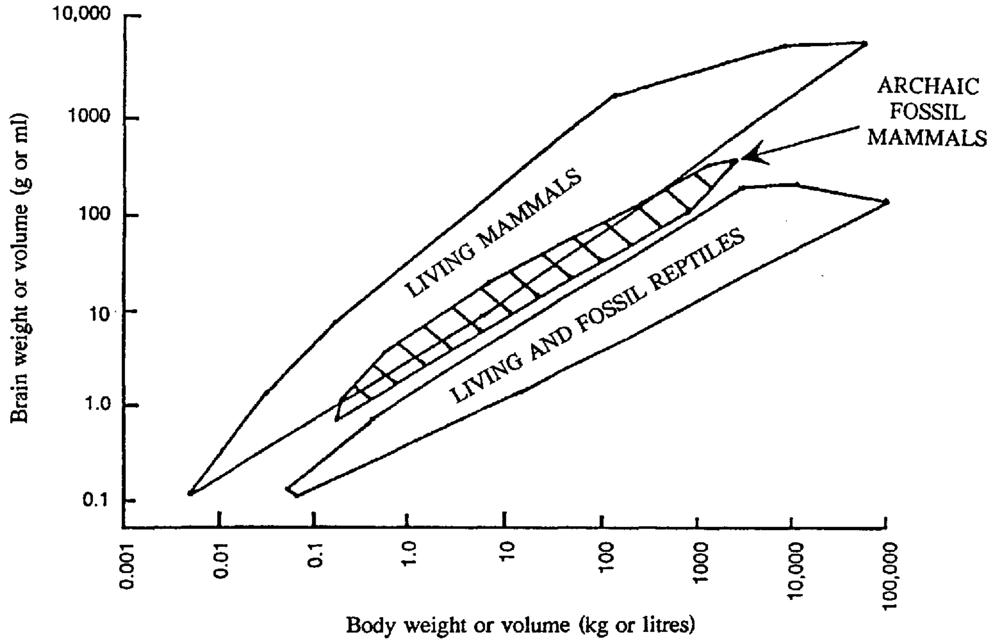

Figure 1 The ratios of brain:body size in modern and archaic mammals; data are presented on logarithmic scales.

(redrawn from Jerison 1973)

The earliest mammals are distinguishable from all other vertebrates in having much larger brains in relation to their body size; this results mainly from the evolution of a new region of the cerebral cortex which is known as the 'neocortex'or 'neopallium'. It is believed that the neocortex is the part of the brain which co-ordinates sensory data and creates a model of the world which determines subsequent action. Jerison (1973) referring to the mammalian brain states 'the simplest intuitive description of the (mammalian) brain's work is that it creates a 'real' world. Within that world all the events of a lifetime take place'. The neocortex is the thinking brain and the mammal relies on it for cognitive concepts of the world in which it lives.

It is surprising that this new type of mammalian brain arose suddenly, by palaeontological standards, alongside reptiles which otherwise were anatomically almost indistinguishable. The reptiles and other vertebrates act mainly by relatively simple responses to specific stimuli and much of their sensory processing, as for example in the amphibian eye, takes place within the sense organ itself. In contrast to reptiles, according to Jerison (1973), 'it was with the evolution of mammals that there evolved the capacity (or necessity) to transform input into output by the intervention of a conscious perceptual world'. No doubt it was this reliance on intelligence that enabled them to survive as small vulnerable members of the fauna for over 100 million years throughout the great age of the dinosaurs long after the closely related synapsid reptiles had become extinct.

Mammals differ from living reptiles in being homoiothermous, which enables the level of neural activity in the brain to be maintained at an optimum functional level despite fluctuations in ambient temperature. It seems very likely that advanced synapsid reptiles were also warm blooded and that this was an essential precursor to the evolution of the mammalian brain.

The intellectual arms race

At the end of the Cretaceous period approximately 60 million years ago, the dinosaurs perished and, subsequently, mammals underwent a rapid adaptive radiation and the age of mammals began. Brain size, however, continued to increase in most of the placental orders including carnivores, ungulates, cetaceans and primates. Figure 2 illustrates the difference in brain size of a modern fox, *Fennecus* from that of an Oligocene fox, *Hesperocyon*, which lived 30 million years ago; not only does *Fennecus* have a larger brain but the surface area of its neocortex has also been increased by elaborate folding.

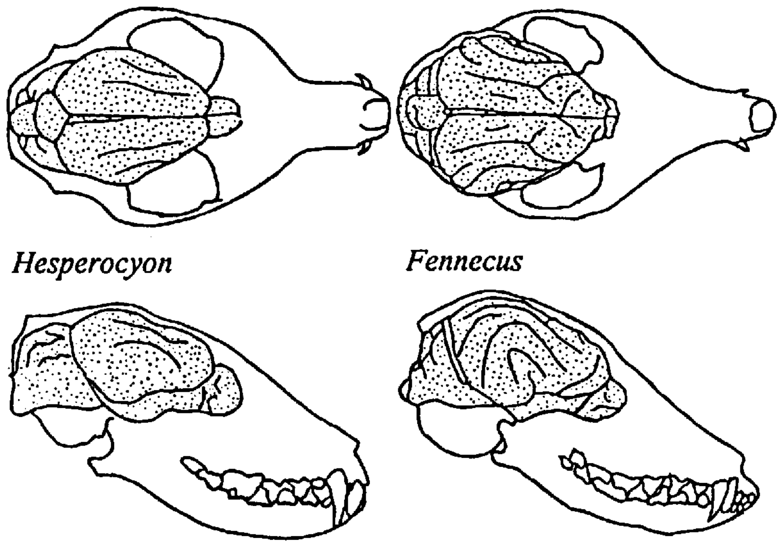

Figure 2 Increase in brain size as illustrated by the endocranial casts of two fox-like members of the family Canidae, the Oligocene *Hesperocyon* and the living *Fennecus*.

(after Romer & Parsons 1977)

Throughout the Caenozoic and Recent periods there has been an intellectual arms race in the placental mammals and natural selection has favoured individuals with greater intelligence. The fossil record clearly shows that there is a strong correlation between the relative sizes of the brains of contemporary carnivores and herbivores. Figure 3 illustrates the progressive increases in relative brain sizes of ungulates and carnivores throughout their evolutionary history.

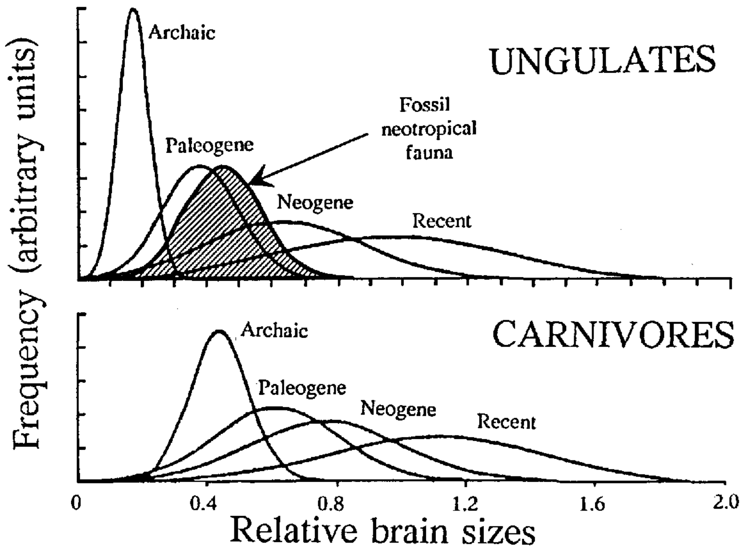

Figure 3 Relative increases in brain sizes throughout the evolutionary history of ungulates and carnivores; showing archaic orders, extinct neotropical orders and members of modern orders from the early Caenozoic (Palaeogene), late Caenozoic (Neogene) and Recent periods.
(after Jerison 1973)

As carnivores became cleverer, herbivores matched them with counter strategy. For example, only an intelligent carnivore would appreciate that 'stotting', which is energetically jumping up and down, by an antelope will give an indication of its vigour and, consequently, its ability to evade capture. There is very good evidence of this arms race in South America. From the Eocene until the Pliocene, South America was an island cut off from the rest of the world. It had a fauna of large placental herbivores (Paenungulata) and marsupial carnivores (Borhyaenoidea); the borhyaenoid carnivores had not shown as great an increase in brain size as their placental counterparts (Fissipedia), in fact their maximum brain size to body-weight ratio was half of that of the average placental. This put less pressure on prey species to increase their brain size, so that when South America ceased to be an island, placental fissipedes invaded and wiped out the small brained paenungulates. The borhyaenoids also became extinct, either as a result of direct competition from the fissipedes, or because they were not clever enough to catch the larger brained ungulates which came in from the north (Jerison 1973). Figure 3 provides data from late Caenozoic neotropical ungulates which show that they had smaller brains than contemporaries elsewhere.

From these examples it is clear that mammals, having evolved the thinking brain were then involved in a highly competitive situation where intelligence and being well informed equated with survival. In other words survival depended upon data collection and analysis and the achievement of goals. This is particularly important for the young because it prepares them for adult life and, in fact, mammals have uniquely evolved childhood and adolescence, which enables individuals to learn and gain information in a protected environment.

The need for information has pressurized mammals into what may seem to us to be apparently unnecessary activity; they actively seek experience and information to build up their cognitive world. This involves a programme of activity and the animal's behavioural needs relate to the acquisition and analysis of information.

The evolution of leisure

Work can be defined as activities concerned with immediate survival, such as foraging. Although work usually has a definite reward, mammals may work more than they need to do, if by so doing they can improve their skills. The foraging monkeys studied by Chamove *et al* (1982) worked for rewards which were strictly superfluous, but none the less enabled them to acquire and maintain their physical and mental skills in detecting hidden food.

Leisure activities, such as play or curiosity, occur when a mammal is not working. Behaviours such as fighting, prey catching or eluding predators cannot be experienced without serious risk, so mammals, from marsupial carnivores, such as the tiger quoll, *Dasyurus maculatus* (Fagen 1981), to human beings act out these scenarios using social play to practise these skills. Efficiency in play may at some later date mean the difference between life and death for the individual. Likewise curiosity about apparently irrelevant stimuli may later prove of value; chimpanzees which play with sticks use them more efficiently as tools compared with those which do not. Curiosity is the process whereby mammals gain information about the properties and utility of unknown objects through sensory investigation, followed by manipulation and experimentation.

It is apparent that leisure activities do not contribute directly to day to day survival, whereas work relates to immediate needs which must be satisfied first. If resources permit, most mammals will carry out both kinds of activity, but work always has the higher priority (Baldwin & Baldwin 1976). Mammals hunger for food, which is essential for survival, but they also hunger for knowledge. Natural selection favours the well informed and those that go out and seek information are at an advantage over the ignorant.

Leisure activities are characteristic of mammals; a reptile, amphibian or fish which is safe, at an appropriate temperature and satiated, is inactive. It does not need to seek stimulation or occupy its leisure time with play or curiosity (this is why zoo reptile houses are generally so boring to the public).

This is not new information, as dates of the references show, but our knowledge of the behaviour of our fellow mammals has sometimes been restricted by the attitudes of those who have studied them.

Scientific approaches to mammalian behaviour

The behaviour of mammals has been studied by three groups of scientists; ethologists, comparative psychologists and primatologists. Ethology arose as a branch of evolutionary biology which was concerned with the animal in its natural environment and its evolutionary position. Ethologists traditionally looked for patterns of behaviour which were relatively fixed in character for two reasons, firstly, so that they could make comparisons between species and, secondly, because such events could be readily replicated and analyzed statistically. This approach was highly successful and worked particularly well for fish and birds so that ethology has tended to concentrate on these groups. As the emphasis was on instinct, learning was largely ignored. Ethological studies on mammals have been mainly concerned with the social aspects of their behaviour because these involve patterns which can more easily be identified and defined; while this is a fascinating area in its own right (Poole 1985), learning and intelligence have been neglected.

In complete contrast, comparative psychologists, while appreciating the intelligence of mammals, were interested in comparing the learning abilities of different mammals and relating them to those of humans. The psychologists' experiments were highly artificial and little attention was paid to the role of learning in the natural environment. Surprisingly, most primatologists have adopted the traditional ethological approach and taken little interest in the animal's use of intelligence in the wild. The emphasis has been on social organization while more flexible behaviours such as learning, play and curiosity have been neglected. There are notable exceptions however, and Byrne and Whiten (1988), de Waal (1982), Goodall (1986) and Matsuzawa (1989) have taken an interest in cognitive ethology which Griffin (1976) urged us to pursue over fifteen years ago.

Our awareness of the behavioural needs of mammals depends on two important considerations; these are the extent to which our own perceptual world overlaps with theirs and, secondly, their ability to communicate these needs to us. When behavioural scientists believe that they are studying mammals objectively, through human perceptual limitations, they are actually being highly selective in sampling visual events and sounds within a narrow waveband, while ignoring most tactile and olfactory signals. This gives a very restricted view of the events which are of greatest significance to most mammals. It is not surprising that we are much better informed about the behavioural needs of primates, which not only share our perceptual world, but are also good at communicating their state of psychological well-being, while the behavioural needs of most other mammals have been neglected.

From both behavioural data and the fossil record, it is apparent that there is a great chasm between the mammals and most other vertebrates with respect to their use of intelligence as a fundamental strategy for survival. Mammals are unique in their reliance on intelligence and their need to create a cognitive world from their experience of data gathering and analysis. Not only is the neocortex capable, as Jerison points out, of sustaining a concept of the real world but, through play and curiosity, even the relatively primitive marsupials seem to be able to create an imaginary world in which they can set up model scenarios and act them out.

A comparison with birds

Those concerned with animal welfare have sometimes equated the behavioural needs of birds and mammals because both are homoiothermous and have larger brains than reptiles. However, it is important to remember that birds are much more closely related to living reptiles than to mammals. The most recent common ancestor of birds and mammals was a primitive, Carboniferous stem reptile living 300-340 million years ago. Furthermore, birds lack the large neocortex and their cerebral hemispheres are also quite differently organized from those of mammals (see Pearson 1972, Romer & Parsons 1977 p 544). Jerison (1973) states that 'birds are just clever reptiles' and suggests that mesozoic birds evolved large brains to cope with the visual analysis of the complex woodland habitat in which they lived. In marked contrast to mammals, the brain sizes of birds have increased very little during the last 40 million years.

The behavioural data also support Jerison's view that birds have perfected the reptilian brain because they have extensive repertoires of innate behaviour. Undoubtedly this is an adaptive trait because an animal which can fly to get away from danger has less need to develop cognitive abilities and a large brain would be energetically expensive and add to weight problems in flight.

However some birds have evolved, through convergence, what may be described as mammal-like attributes. For example certain members of the crow and parrot family and Australian magpies (Cracticidae) show activities which resemble mammalian social play and exploratory behaviour (Fagen 1981, Pellis 1981a,b). Some birds also show remarkable learning abilities, for example grey parrots have been taught complex discrimination and seemingly, even language skills (Pepperberg 1990).

Because some birds have well developed learning abilities, however, we should not jump to the conclusion that they have psychological needs. As Jerison (1988) has pointed out, learning is a fundamental property of all nervous systems, whereas the intelligence which mammals have evolved is a way of knowing. He also argues that 'the work of the (mammalian) brain is correctly thought of as creating a real world. That act of creation is essentially the same as cognition'. Whether birds have similar cognitive abilities remains to be seen. If some birds really do create an imaginary world in play, it would seem to imply that they also have constructed a real world in their brain.

Classifying behavioural needs

The psychological well-being of mammals depends upon the existence of facilities for information gathering and their analysis. Without these opportunities, the mammal's welfare is seriously compromised. Only mammals are known to experience boredom and psychological distress in a situation where all their physiological needs are met. In general, European ethologists (including myself) have tried to fit mammalian behaviour within the framework of traditional ethology, an approach which has been so successful with lower vertebrates and birds. We have sought constancy of pattern and easily replicated activities, such as threatening, mating and courtship, which are common to most vertebrates. Thus we have tried to reduce the mammal to a machine-like model. Because ethologists have failed to investigate the ways in which mammals are unique and flexible in their behaviour, they have experienced difficulty in understanding the theoretical background to their behavioural needs. I believe that the Americans are correct to use the term psychological well-being for primates, rather than ethological needs, but that it should be applied to other mammals as well.

It is apparent that all vertebrates have behavioural needs, but that mammals differ because they suffer psychologically if their behavioural needs are not met. In view of the fact that the terminology in current use is confused, behavioural needs, ethological needs and psychological needs are attributed to animals but none are clearly defined. On the basis of this analysis of behavioural needs, I suggest the following classification:

Behavioural needs

This is a general term which refers to any requirement which an animal may have to carry out activities ranging from a single behavioural act to a complex programme. Behavioural needs can be subdivided into two categories:

Psychological needs refer to the needs of the mind and appear to be peculiar to mammals. They are a requirement on the part of the individual to acquire experience which enables it to collect information and analyze it, to build up a cognitive picture of the world in which it lives and to act on this knowledge. If, through confinement in an over simplified environment, mammals are unable to satisfy these needs, they are aware of the deprivation and experience psychological distress. Psychological needs relate directly to the concept of psychological well-being which is an attribute that appears to be unique to the mammalian mind. Psychological well-being is more than the absence of distress, it is a positive state of mental satisfaction resulting from the animal's psychological needs having been met.

Ethological needs are specific requirements for a particular stimulus or type of material which enable animals to carry out certain behaviour patterns or sequences of patterns. Deprivation will simply result in the animal not being able to display the behaviour and, unless this directly affects its survival or causes physical discomfort, the individual will not suffer from the lack of the facility. This kind of need is simply a question of what is required to do a particular job; it does not imply that the animal experiences a need to do the job in question. Ethological needs are not the same as psychological needs. A toad may need to have moving prey, a fish facilities to build a nest, a reptile a facility to sun itself or a bird the opportunity to dust bathe. Satisfying these ethological needs releases sequences of innate behaviour, but there is no evidence that the absence of an appropriate facility compromises the individual's well-being.

From these definitions it would seem that psychological needs are essentially mental needs, generated by the neocortex; they relate to the individual's expectations and its concept of reality. In contrast ethological needs are operated through the evolutionarily more ancient brain regions which control the performance of innate behaviours. The brain operates as a unity (Jerison 1973), so that mammals experience both psychological and ethological needs and, in some cases, the two may be so closely interlinked that they are difficult to categorize. Like most biological classifications, there are likely to be some grey areas between the two kinds of behavioural needs which I have defined.

Conclusions

The need of mammals to carry out a programme of activity relates to their evolutionary history. They succeeded, in the face of competition with large well-armed reptiles, through the evolution of the neocortex which enables them to create a mental image of the real world and to use this knowledge intelligently.

This new mammalian brain has been refined and improved by 60 million years of competition with other mammals in an intellectual arms race. This requirement 'to create in the brain a real world within which all the events of a lifetime take place' (Jerison 1973) is the explanation for such animals as the wolf, monkey or bear having complex psychological needs. Natural selection has caused these animals to experience a need to collect and analyze information. Only by doing so will they experience a state of psychological well-being. Evolution has provided the wrong programming for mammals to settle down contentedly in an enclosure with only the bare necessities provided for physical survival.

When we keep a mammal in captivity, if its welfare is to be ensured, it should be provided with the facilities to implement an appropriate programme of activity which meets the four general requirements which I have described. We must get away from the idea that one piece of equipment represents 'environmental enrichment'; only the facilities to carry out an adequately complex programme will really suffice. Within this programme there should be opportunities to work and also for leisure activities such as play and curiosity.

In terms of practical improvements to animal welfare, I have put forward this theoretical approach in an effort to provide a rational framework on which the behavioural needs of mammals can be based. What may be new is the concept of ensuring psychological well-being by providing facilities for a programme of activity as opposed to piecemeal environmental enrichment which simply offers opportunities to carry out particular behaviour patterns or eliminates abnormal behaviours. By using this more positive approach, the effectiveness of any particular form of enrichment or type of enclosure design can be assessed in terms of its contribution to the particular mammal's programme of activity.

Different species of mammals may have different requirements so that further research is needed to determine what these may be. Comparisons with field studies of the same, or in the case of domesticated animals, closely related species, will help to determine the kind of programme which the animal follows in nature and its components in terms of meeting the individual's behavioural needs.

For guidelines or legislation on the housing of mammals, I should like to suggest something on the following lines:

'Those responsible for the care of mammals should ensure their psychological well-being by providing facilities for an appropriate programme of activity which meets the animal's requirements for:

- *stability and security;*
- *appropriate complexity;*
- *an element of unpredictability;*
- *opportunities to achieve goals.*

Within this programme opportunities should be provided for both work and leisure activities.'

This form of words could replace the present vague requirements for the provision of 'psychological well-being', 'meeting ethological needs' or 'freedom to carry out most normal patterns of behaviour'.

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