The usefulness of behaviour studies in developing captive breeding programmes for mammals
[Plate 2]

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Adequate planning for the long-term captive propagation of exotic species can only proceed with background knowledge concerning the natural behaviour of the species. The planning of breeding programmes also demands that certain essential parameters of life history be known, such as age at puberty, duration of reproductive capacity, and maturation rate. Some demographic data of this type can be obtained only by long-term field work. Unfortunately, there are too many species which have been maintained unsuccessfully in zoos, the failures in part resulting from a lack of knowledge of the species' natural history. With some basic information, preliminary captive studies may be carried out, but careful monitoring of a captive population must be done to detect pathological abnormalities, which may be conveniently subdivided into four categories: behaviour, nutrition, reproduction and disease syndromes. Obviously there will be overlap; nutritional problems may manifest themselves in both reproductive failure and debilitation, and thus affect behaviour.

A species or subspecies in nature consists of discrete populations which show relative degrees of inbreeding. The term species is an abstract concept based on averages of the component populations' characteristics. All species show a range of adaptational plasticity, which in some cases may be quite narrow and in others quite wide. Genetic differences in the founding stocks of species held in separate institutions can occasionally provide an explanation for differential success in captive propagation, even with the adoption of almost identical maintenance techniques. These potential genetic differences within a species must be accepted as a possible cause of behavioural differences.

In this paper we will confine ourselves to the origin and interpretation of behavioural pathologies and the possibility of predicting behaviour from captive studies. Abnormal behaviour can be

induced because space requirements are not being correctly met. The improper composition of the social unit which serves as the breeding nucleus may also affect behaviour and cause reproductive failure. The resulting social stresses may show themselves as failures in reproductive function or parental care. Finally, behavioural pathology may result from a failure by curators to replicate essential niche requirements, such as diet, cage artifacts, or nesting facilities.

SPECIES-SPECIFIC RESPONSES TO
CROWDING AND THE QUESTION OF SPACE
Because rodents generally have a short generation time and their space requirements are smaller than those of larger mammalian species, the bases for many theoretical generalisations concerning space requirements have been derived from the investigation of rodent populations. The comparative study of several species of rodents exhibiting different adaptational syndromes has allowed the description of certain behavioural phenomena which are associated with social tolerance and space requirements. The recognition of these behavioural pathologies became the basis for several testable hypotheses which were then applied to other mammalian taxa (Eisenberg, 1967, 1969). For example, in some rodent species which were established in cages as pairs (with adequate shelter, food and water), recruitment through births resulted in the development of rather large populations, followed by the cessation of reproduction. The point at which population increases ceased varied from one species to another. It was proposed, on the basis of these colony growth experiments, that a typical social organisation could be described for a given species' population in nature and that populations exhibiting different social tendencies would respond differently to the stresses of crowding when taken into captivity. Eventually even the most social species could be stressed by crowding, but their thresholds for the exhibition of various forms of pathological behaviour were higher than those of species or populations which were adapted to a more solitary or dispersed existence (Eisenberg, 1967). It was also suggested that, although the maximum population size could be higher in larger cages, the actual density at which reproduction terminated would remain about the same in a given species.

When solitary species are given sufficient space, they only exhibit close contact with conspecifics during the oestrous period or during the rearing of young. Although such species can coexist as pairs in captivity, when held in this fashion reproductive failure is common; the ♀ may not conceive or the normal rearing pattern is disturbed. Reproduction is successful only when the ♀ is removed from proximity with the ♂ except for the mating period (Eisenberg, 1967).

Social species which normally exist in groups will breed in close confinement, but reproduction will eventually be curtailed, often because the young born to the founding pair have become 'psychological castrates'. A family group may exist with no overt aggression or tension, yet reproduction will be confined to the founding ♀ alone or her oldest daughters. With rodent populations in limited space such psychological castration may be irreversible (Calhoun, 1963). Thus, even social species which remain peaceful in a group context must be periodically segregated in order to promote maximum reproduction from the descendants of the founding pair.

Recent research (Krebs et al., 1969; Myers & Krebs, 1971) on the population dynamics of voles of the genus Microtus indicates that the question of population growth and decline in nature may be accompanied by subtle genetic changes. As is well known, in the temperate zone, microtine populations undergo periodic oscillations. One of the early observations on the nature of such population fluctuations included the fact that at the end of a population crash a certain recovery period was necessary before the population increased again.

At first such a lag in reproduction was assumed to be the result of alterations in the habitat which reduced the overall carrying capacity. Later research suggested, however, that some qualitative change in the population occurred as a result of crowding (Chitty, 1957). Chitty (1960) hypothesised that the alterations in microtine populations as a result of crowding may have resulted from intensive selection for certain genetic strains present within the microtine populations during the period of population growth. In short, several genetic morphs normally exist in a natural population, but during crowding selection for an especially aggressive phenotype could

result in an altered genetic structure of the population at the time of the population crash. If the reproductive capacity of the aggressive genotype differed, it would explain the lag in recovery of the population.

Of course, an alternative explanation might be that the altered early experience of young microtines born under high densities affects not only their social relations but their reproductive rate. Krebs *et al.* (1969) have demonstrated that different behavioural morphs may predominate at different phases of population cycles in voles and, furthermore, that differences in certain genetic characters appear during the phase of population increase.

The implication of the research on microtines for captive propagation are quite clear. Whether genetic or induced by early experience or both, such behavioural alterations may well exist in other mammalian populations. Thus, when individuals are brought into captivity from a population whose structure is unknown, there is a definite probability that the preselected genotype may not be the most successful genotype for long-term captive propagation. On the other hand, the very existence of different behavioural morphs in nature (which may be the result of natural selection through population fluxes) suggests immediately that selection from the wild population for genotypes most amenable to captive propagation is also possible.

In the course of domestication or adaptation to captivity, the husbandman usually selects, on the basis of behavioural phenotype, those specimens which appear to be the most compatible with the captive condition. This may facilitate the conversion of an exotic stock to a captive propagating population but continued selection for constancy in a morphological phenotype may affect the behavioural phenotype so that after some generations the resulting population could not exist in the wild, should release be considered. It is obvious that the husbandman should be aware of changes induced by active selection in the conversion of an exotic to a captive propagating population.

SPACING REQUIREMENTS AND INTERNAL CAGE STRUCTURE

Hediger (1950, 1955) emphasised the importance of space in the adaptation of animals to captivity and developed the concept that there is a 'flight distance' for each species. He stressed that enclosure size must take this into account so that an animal was not always in a state of fear. Hediger also discussed the importance of psychological space and how the appropriate use of cage furnishings can increase the space available to an animal. Thus, for some species, a large empty enclosure may be less desirable than a small one complicated by many artifacts.

An understanding of the animal's movement patterns in nature is fundamental to the design of effective housing (Hediger, 1950, 1969). Hediger (1950, 1955), Meyer-Holzapfel (1968), and others have described in detail the effects of enclosure size and shape on behaviour, including the development of stereotyped movement patterns. The zoo literature is replete with behavioural descriptions of how animals respond to cages, yet there are no detailed studies of the development of stereotyped patterns or of the loss of such behaviour through manipulations by animal managers. A careful investigation along these lines would be of great use in the development of cage design, particularly in species where stereotyped movements may become so fixed that they are likely to affect propagation.

Specific niche requirements are as important to successful maintenance and propagation as absolute space. For example, the number of denning sites or nestboxes is often critical. As outlined by Martin (1968, 1975), at least two nestboxes are a prerequisite for sustained captive propagation in the tree-shrew *Tupaia belangeri*. Normally a pair sleeps in one nest and the ♀ gives birth in a separate nest. She does not, however, brood her young in the natal nest but continues to use a separate nest with the ♂. If only one nestbox is provided, cannibalism of the young is common. If two are provided, spectacularly better propagation results.

A similar need for multiple nesting sites has been observed in the Red panda *Ailurus fulgens*. Before the birth a natal nest is chosen and often lined with leaves. However, the ♀ tends to move the young frequently and, if insufficient nesting areas are available, she may carry them around in her mouth excessively (Roberts, 1975). Such behaviour can, of course, result in the young being dropped and killed or deformed by excessive carrying by the neck. A periodic tendency

to change the location of the maternal den has been observed in captive wolves *Canis lupus* and may well occur in many carnivores in nature, especially as the young become more mobile and litter accumulates in the den. In captivity such behaviour may also be a response to the constant stress of confinement, but the provision of several nesting sites can prevent cannibalism or other pathological behaviour directed towards the young (Plate 2).

In the wild, agouti *Dasyprocta punctata* young hide in nesting sites too small for an adult to enter (Smythe, 1970). This behaviour is reminiscent of those ungulates termed 'hiders' (Lent, 1975). Immediately after birth the mobile young chooses an appropriate nest, such as a narrow hole, and remains there while the mother forages alone, returning only to nurse. The infant emerges from the nest only when called by the ♀ with a specific vocalisation. After several weeks, the young begins to follow the mother. We have observed similar behaviour in captive acouchis *Myoprocta pratti* when a narrow tube, which only young could enter, was provided. Such artifacts may well prove important in captive propagation of these species.

Niche requirements are often not obvious and, in the absence of field data, frequent manipulations of cage artifacts may be necessary before a final cage design can be adopted. The Giant panda *Ailuropoda melanoleuca* spends little time autogrooming by licking, nibbling, or scratching its dense fur, which appears to be conditioned by sand and water bathing. When allowed on a grass substrate or supplied with tubs of soil, the panda will rub and writhe while lying on its back on the soil; the underside will be cleaned by rubbing with clods of soil or sod, using the forepaws. When water is available, the animal may also bathe daily and it is likely that the absence of both soil and water will result in poor fur condition.

MEETING SOCIAL REQUIREMENTS

Observations in the field suggest that each vertebrate species has a typical social structure. For example, in mammals there are species with individually defended home ranges with virtually no overlap between a ♂'s home range and that of a ♀ throughout the greater part of the year. Such species exhibit a dispersed social organisation and are solitary, an example being the American red squirrels of the genus *Tamiasciurus* (Smith, 1968). On the other hand, some species of mammals typically show pair bonding and the activities of the ♂ are important to the normal rearing of the young. Such cases have been described for primates of the genera *Cebuella*, *Saguinus*, *Leontopithecus* and *Callithrix* (Epple, 1975a). An arrangement whereby the ♂ in a pair-bonded species provisions the young and the ♀ during lactation may be found in several genera of the Carnivora and in particular in the canids, *Vulpes*, *Canis* and *Cerdocyon* (Kleiman & Eisenberg, 1973; Kleiman, in press). Other mammalian species, such as the Indian elephant *Elephas maximus*, exist in larger social groupings whose core organisation is based on a matriarchy (McKay, 1973).

Obviously, knowledge of the various forms of social structure enables the planning of a captive propagation programme where an approximation to the natural social structure can be sustained. Although it is best to have and use data as described in nature, there are examples where the actual determination of social structure evolved by trial and error from captive studies.

Among callitrichids, for example, a founding pair was often allowed to develop through births into a large family group. Although behaviourally stable, only the initial pair would ever breed; thus reproduction was limited. Such groups could remain stable for many years (Epple, 1970, 1975b; Rothe, 1975). The periodic removal of adolescent young and their establishment as new pairs releases the reproductive inhibition and is essential to an effective callitrichid propagation programme. Although confirmatory data are not available, it has also been suggested that neighbouring family groups in visual contact may exert inhibitory influences on each other, with one pair (or family) emerging dominant and exhibiting the only successful reproduction (Snyder, 1974). The suggestion that these animals are probably monogamous has recently been supported by field studies (Dawson, in press; Neyman, in press). Had the field data been available ten years ago, it is probable that the captive population of endangered species such as *Leontopithecus rosalia* would now be larger (see also Kleiman, p. 95).

Where field data are available for one species, there may be a tendency to apply that information

to the management of a second closely related species, but such application may often be inappropriate. For example, a knowledge of the social structure of Burchell's zebra *Equus burchelli* really does not assist in planning for the captive management of Grevy's zebra *E. grevyi*. As Klingel (1972) has shown, Burchell's zebra has a social organisation built around a polygynous mating system. One stallion defends and guards a group of mares. As ♂ offspring mature, they move out and become peripheral to the basic polygynous unit. Thus a captive propagation strategy would involve leaving a single stallion with a group of mares and culling young ♂ offspring at approximately two years of age.

If this same system were applied to Grevy's zebra, failure would result through mild aggression among ♀♀ and strong aggression between sexes. In nature Grevy's zebra does not have a permanent harem system. Reproductive ♂♂ stake out territories at traditional sites and defend them actively against one another. When in oestrus, mares wander into the ♂ territories where they are actively courted. After mating, they leave the territory; mares with offspring tend to forage individually. Thus, there is no permanent association between a stallion and a mare or even a group of mares, and herds, when they are formed, are often of a transient nature (see also Dolan, p. 30).

Another example where reproductive failure has been caused by inappropriate management of social structure is the cheetah *Acinonyx jubatus*. Unlike the other large and small cats (except the lion *Panthera leo*), cheetahs are easily and compatibly maintained in pairs or groups in captivity. However, unless such a group is provided with sufficient space for complete ♀ isolation, successful breeding rarely occurs. Although there have been many suggestions concerning the social requirements of captive cheetahs for successful propagation, including the need to have more than one ♂ for competition (Curtis, 1972; Herdman, 1972; Eaton, 1974), it appears that the single most important factor is the isolation of the ♀ from all conspecifics, except for breeding. Whipsnade Zoo has followed this policy and probably has the longest and most successful cheetah propagation programme of any zoo (Manton, 1975). The need for isolation derives from the fact that cheetah ♀♀ normally forage alone, except when with older cubs, and do not commonly associate with ♂♂ (Curtis, 1972). Grouping cheetahs in captivity, even in a pair, results in habituation and reproductive inhibition.

The behaviour of a single ♀ cheetah which had been living for four years with a ♂, but had not reproduced, was recently analysed by Kleiman & Robinson (unpublished). The ♀ was more active (more pacing) and urinated less frequently in the ♂'s presence. Moreover, her behaviour, especially the pacing pattern, was more stereotyped when she was with the ♂. This difference suggests that she was under more stress and her territorial behaviour was inhibited with the constant association.

QUESTIONS OF DIET

Although an experienced morphologist can in part determine dietary requirements from dentition and gut morphology, no single aspect of captive maintenance is more dependent on field data than the question of food selection. Especially troublesome in captivity are herbivores which are adapted for feeding on leaves. The difficulties in the captive maintenance of such mammals as the koala *Phascolarctos*, the three-toed sloths *Bradypus* and many of the leaf-eating monkeys *Nasalis*, *Colobus*, and *Presbytis* are well known. The spectacular physiological and morphological adaptations of arboreal leaf-eating mammals have been the subject of a recent symposium (Montgomery, in press). As field data accumulate for such species as the three-toed sloth *Bradypus infuscatus* (Montgomery & Sunquist, 1975), it becomes more apparent that the exact replication of a natural diet may be almost impossible and we are confronted with the problem of dietary conversion. All experience suggests that in these delicate species this is best accomplished with juvenile animals or animals which are at the point of adapting to the adult diet. Even then, it is difficult to prepare adequate diets which match the pre-adapted requirements of the digestive process for the species in question (Roberts & Collins, in press).

Aside from the attendant problems of food selection, the way the food is presented may have a profound effect on the animal's health. Small carnivores which normally kill their prey in isolation from the group may be severely stressed if forced to eat in proximity to one another. The

simple procedure of separating individuals at the time of feeding, even if they live compatibly in the same cage, is well known. Where an animal habitually eats its food is often an important consideration in the designing of cages. For example, small carnivores, which prefer to eat their prey in seclusion, need to have some artifact or barrier, to give at least an illusion of isolation. The size of the food items may be critical. Marmosets and tamarins eat best when provided with food in bite-sized chunks.

DEMOGRAPHY

In this brief review, we also wish to emphasise the importance of an understanding of natural demographic variables for adequate captive propagation. It is well established that animals with greater longevity often produce small litters and have the capacity to reproduce over several seasons (Eisenberg, 1975). Species which typically have large litters and early maturation often become reproductively senile in a very short span of time. Thus, the preparation of a simple survivorship curve for a species in nature should give some clues as to the type of breeding programme which is necessary. With species that reproduce rapidly, it is necessary to develop the programme with the F_1 generation. A delay in breeding offspring may be fatal for the long-term existence of the colony. Since most small mammals have a short life/large litter correlation, the propagation of small mammals in captivity over a long period often demands sound management with the removal of young at an extremely early age to establish new founder groups.

A study of survivorship curves, such as that developed by Dittus (1975) for the Ceylonese Toque macaque *Macaca sinica*, is very instructive. Dittus' data clearly show different periods of vulnerability for newborn ♂♂ and ♀♀. Females experience an early severe mortality in nature, but once they reach adult status their prospects for sustained longevity are excellent. On the other hand, young ♂♂ are protected from early mortality by older ♂♂ and their initial survival rate is good but becomes acutely depressed when they become subadult. The net result is that the number of adult ♂♂ is smaller than adult ♀♀ in the population but the survivorship potential during the developmental years is quite different.

An understanding of the demographic difference in survivorship can help elucidate captive pathologies. In short, it may be anticipated that under captive conditions young ♀♀ *Macaca sinica* in a group situation may be more severely stressed than young ♂♂, with the result that ♂ survival may be much better even into adulthood than that of ♀♀. The knowledge of natural survivorship curves and the behavioural mechanisms underlying differential survivorship should improve the development of appropriate management techniques for confined populations.

THE FUNCTION OF CAPTIVE BEHAVIOUR STUDIES

Until recently, the study of the behaviour of animals in zoos had been concentrated in Europe, and many significant advances in the discipline of comparative ethology had emerged from zoos in Great Britain, Holland, Switzerland and Germany. It is not, therefore, surprising that the major periodicals and journals in which studies of captive exotic animals appeared were also based in Europe; examples include *Der Zoologische Garten*, the *International Zoo Yearbook*, *Zeitschrift für Tierpsychologie* and more recently, *Applied Animal Ethology*.

The topics studied in exotic zoo animals have included those most amenable to the captive condition. Comparative studies of closely related species have been common and here emphasis has been placed on the evolution of behaviour (Leyhausen, 1956; Kleiman, 1967; Van Hooff, 1967; Wemmer, in press). In other studies, particular categories of behaviour have been investigated in diverse species, including eliminative behaviour (Altmann, 1969), drinking (Schönholzer, 1959), Flehmen (Schneider, 1930), predatory behaviour (Eisenberg & Leyhausen, 1972), play (Meyer-Holzapfel, 1956) and vocalisations (Tembrock, 1963). Finally, investigators have concentrated on the behaviour of single species, sometimes following known individuals for many years, e.g. *Ateles fusciceps* (Eisenberg, 1976), *Tupaia belangeri* (Martin, 1968), *Canis lupus* (Schenkel, 1947, 1967), *Dolichotis patagonum* (Dubost & Genest, 1975). Such studies often concentrated on social structure and social behaviour.

Comparative ethological research has often elucidated essential requirements for the

maintenance and propagation of exotic species. Martin's (1968) study of *Tupaia* is a well-known example. Other studies have already been alluded to. Thus, captive behaviour observations may not only function in the development of theory concerning the evolution of behaviour, animal sociology, etc. but can provide the basis for sound maintenance.

Such behavioural studies are important mainly because of their predictive value. Much of ethology and comparative psychology is concerned with defining the probabilities that an animal will perform a certain act at a given time but variations in performance arise both from external variables and individual differences. If these can be identified then behavioural changes may be more predictable and, when abnormal behaviour patterns arise, their origin may be more rapidly found. Thus, whatever the apparent rationale for captive behaviour studies, they do provide a norm from which deviations may be measured. Kleiman (1974a, 1974b, 1975) has discussed methods which can be used by keepers, students and volunteers for recording behavioural data so that observations are standardised.

The depth of the observations depends on the complexity of the perceived problem and the desired outcome. For example, tigers *Panthera tigris* like many other felids exhibit certain clearly defined behaviour patterns when in oestrus and a simple check-sheet with limited observation time may be used to determine when the sexes should be introduced (Kleiman, 1974a). However, oestrous behaviour in the Indian rhinoceros *Rhinoceros unicornis* may be more subtle, requiring the evaluation of numerous behaviour patterns from long-term observations if the pair are put together only for breeding (Buechner & Mackler, 1976).

The importance of defining oestrous behaviour in a healthy reproductive ♀ becomes apparent when it is necessary to determine the causes of infertility in another ♀. The changes that are known to occur with oestrus can be used to illuminate the causes of malfunction should they be behaviourally based. Of course, the behavioural abnormality may only be understood when examined in the light of adequate data. One of the most frustrating facts with which curatorial staff live is the limited available information on the behaviour of the species in their care. The

individual variations in behaviour within a species and the all too few specimens of so-called important species available for study limits the ability of zoo personnel to detect behavioural pathologies and find solutions for them.

For example, in attempting to determine why a habituated pair of cheetahs may not breed, one needs a behavioural profile of cheetah ♀ behaviour for comparison. The data base, however, does not exist as yet. The collection of even the most detailed behavioural information on one pair of Giant pandas may be insufficient to explain behavioural differences that exist in a third specimen. Thus, although captive behaviour studies are essential to develop behavioural norms or profiles to allow zoo personnel to predict expected changes or detect abnormalities, the variability in individuals must always be kept in mind.

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