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William C. McGrew
University of Stirling

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Recommended Citation

McGrew, W.C. (1981). Social and cognitive capabilities of nonhuman primates: Lessons from the wild to captivity. *International Journal for the Study of Animal Problems*, 2(3), 138-149.

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Social and Cognitive Capabilities of Nonhuman Primates: Lessons from the Wild to Captivity

William C. McGrew

All anthropoid primates in nature lead highly sociable lives. In infancy and childhood this is characterized by stability and familiarity for both sexes; in adulthood either one or the other sex changes groups. The natal group provides a social network of matrilineal kinship; after sexual maturity incest avoidance and exogamy are the rule. Important differences exist across species and between the sexes in mating strategies. In most species, males emigrate, but in others females do so. Male sexual behavior is based on competition between peers; females exercise choice in selecting sexual partners. Normal development of sexual behavior and maternal caretaking requires contact with adults. According to one school of thought, the selection pressures of dynamic life in groups led to the evolution of "social intelligence." Such cognitive abilities are manifested in coalitions and reciprocity based on assessment of the predictability of others' behavior over time, i.e., on long-term relationships as well as short-term interactions. Another school of thought sees the evolutionary origins of cognitive capacities in the demands of subsistence. "Extractive" foraging requires varied techniques for the acquisition and skillful processing of foods. Optimal budgeting of daily activities such as ranging is facilitated by long-term memory and cognitive mapping. The absence of such social and environmental challenges may lead to pathological behavior.

Introduction

Like all other organisms, nonhuman primates are products of evolution by natural selection. That is, selective pressures in the physical and social environment have shaped the form and function of the organism through variation in reproductive success. Such selection has acted both on the primate's structure and on its behavior, and the two are inextricably linked (Clutton-Brock and Harvey, 1976). Even those behaviors which are cultural in nature, i.e., those transmitted by social learning from one individual to another, are ultimately limited by the capacities of the brain, which is a construction of the genome (Bonner, 1980).

This state of affairs has obvious implications for anyone seeking to learn from nonhuman primates in captivity. This will apply both to those studying primates for their own sake and to those using primates as a means to seek solutions to human problems. In either case, the validity and reliability of research into normal processes will be enhanced in direct proportion to the resemblance of conditions in captivity to those in nature. Moreover, it follows that measures to safeguard mental health in captive primates should take equal precedence to those concerning phy-

*Dr. McGrew is Lecturer in the Department of Psychology at the University of Stirling, Stirling FK9 4LA, Scotland. This paper was prepared for and presented at the Institute for the Study of Animal Problems symposium on Nonhuman Primates in Biomedical Programs, 15 October 1980, San Francisco, California. Previously published symposium papers: J.R. Held, Breeding and Use of Nonhuman Primates in the USA and A.N. Rowan, Scientific Issues and Regulation of Primate Use (*Int J Stud Anim Prob* 2(1), 1981); A.A. Eudey, Ethical Concerns in Primate Use and Husbandry (*Int J Stud Anim Prob* 2(2), 1981).*

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Figure 1 Three male chimpanzees engage in quiet, social grooming.

sical health. Finally, the plasticity of primate behavior is not without limits, and research procedures that push subjects beyond those limits run the risk of distorting or even nullifying the results obtained. In short, lab and zoo workers should listen to field workers, for they sometimes can supply crucial knowledge. (Of course, the reverse may also be true, but that is the subject for another paper).

Relationship Between Field and Laboratory

What has been said so far is not new, and the gap between field and laboratory is not nearly so wide as sometimes has been supposed. One of the few advantages of the shrinkage in job opportunities in the 1970's was that a sizeable number of field primatologists found themselves in laboratories, and a number of laboratory workers ventured to the field. Cross-fertilization ensued. Furthermore, over the same period, a number of institutions and individuals founded facilities which represent a compromise between the extremes of cage and canopy. Such free-ranging

populations, usually housed outdoors in relatively spacious, semi-natural surroundings, range from fenced or moated enclosures in safari parks (Pfeiffer and Koebner, 1978) to off-shore islands (Estrada and Estrada, 1976). Many lessons learned from early field studies have been applied beneficially to both parties, *i.e.*, to the profits or findings of the human primates and to the increased health and reduced suffering of the nonhuman primates. If this is the case, what then is the justification for this paper? Has it all been said before, and have the appropriate lessons been learned?

In my opinion, the answer to these questions is no. There are at least two major reasons for continuing to pursue the application of knowledge from the wild to captivity. First, in spite of trends to the contrary, the majority of the thousands of non-human primates in captivity still live in pathogenic conditions. Most monkeys and apes in laboratories and zoos are housed and treated such that their mental and physical health suffers as a result. This is especially regrettable, for many of these pathogenic conditions persist through ignorance and could be remedied. The *status quo* is thus unacceptable. Second, a more mundane reason for this article is that new findings accrue constantly, requiring repeated revision of our knowledge of primates. Much of this alteration is minor, but occasionally major surprises require us to reconsider generalizations about a given species or an established procedure. Often these new findings take too long to percolate through to users of primates in the 'real' world; they are published in academic journals or books by scientists unable or unwilling to recognize their practical implications. None of what follows is totally new, and some of the findings are re-interpretations, but they result largely from studies done in the last five years.

Before proceeding, let me try to answer any skepticism aroused by these provocative generalizations with a specific example. It is simple but illuminating. Last year, a large British company that breeds monkeys reported findings which stimulated national interest and eventually caused questions to be asked in Parliament. This study (Welburn, 1979) compared the responses of two species of macaques, *Macaca mulatta* (rhesus monkey), and *M. fascicularis* (longtailed or cynomolgous monkey), to over-wintering in unheated quarters in southern England. The results were dramatic: All of the rhesus monkeys survived, but 85% (22 out of 26) of the longtailed monkeys died. No details of post-mortem examination were presented, but it seems likely that the monkeys died from exposure after much suffering. An important lesson about species differences was learned, at the greatest possible cost to the participants, and at no little financial expense to the firm. What is regrettable is that attention paid to field studies of the two species would have yielded the same knowledge. Recent field work in Borneo, Sumatra and Malaysia shows that the longtailed monkey is a lowland species reaching its highest densities in warm, mangrove swamps (see review in Lindburg, 1980). It is doubtful that the species in nature ever encounters subfreezing temperatures, and its long tail is singularly unsuited to conditions of possible frostbite. On the other hand, rhesus monkeys live in the foothills of the Himalayas, reaching elevations of over 3000m. Their chunky builds, thick coats, and shorter tails all indicate adaptation to colder temperatures. Had these differences been appreciated, much waste could have been avoided.

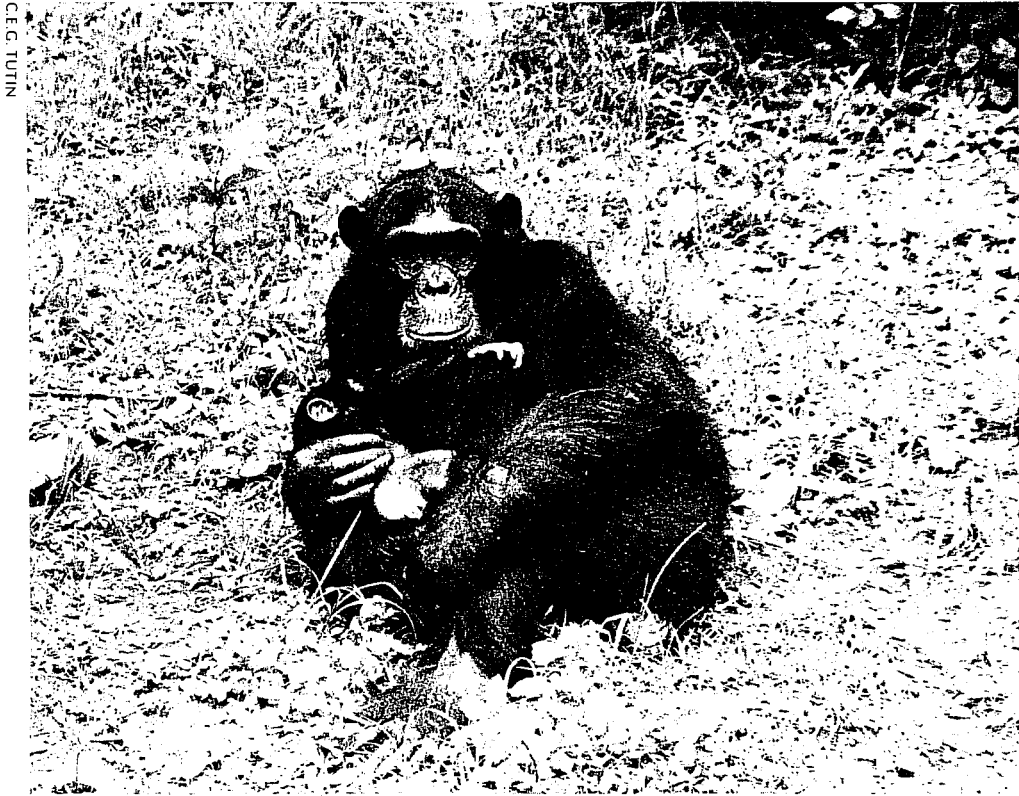
The aims of this paper are, first, to skim over a variety of topics in the general area of social development and organization over the animals' life-span. Second, I shall seek to relate these to cognitive capacities by referring to two types of explanation for the evolution of intelligence. One school of thought credits the selective pressures of dynamic life in groups as the main forces leading to the evolution of so-

cial intelligence. Such abilities are based not only on individual recognition of one's fellows but on predicting their behavior under a variety of conditions over time (see, e.g., Humphrey, 1976). The other school of thought sees the evolutionary origins of complex cognitive capacities in the demands of subsistence, especially feeding. So-called "extractive" foraging requires varied techniques for the acquisition and processing of foods that are irregularly distributed in time and space (Parker and Gibson, 1977 & 1979). Third, throughout I shall make practical suggestions for the husbandry of primates which arise from the new knowledge from field studies.

Social Development and Organization

Primates are sociable (Fig. 1). This may sound like a truism, but at least three points need to be made: Even species that do not live constantly in groups lead active social lives. Such supposedly solitary species are not so, especially as subadults; they differ from other, truly solitary mammals in this regard. This has emerged from studies of orangutans (*Pongo pygmaeus*) in Sumatra, bush babies (*Galago senegalensis*) in South Africa, and tree shrews (*Tupaia glis*) in India. Second, in some such species, previous studies may have exaggerated the solitariness by studying populations under abnormal conditions, e.g., when risks from predators are absent. Wild chimpanzees (*Pan troglodytes*) at Mt. Assirik in Senegal rarely are alone, while solitary chimpanzees are commonly reported at Gombe in Tanzania. The Senegalese chimpanzees are under pressure from 4 species of large carnivores (Tutin *et al.*, 1981) while the Tanzanian chimpanzees are in no such danger. Similarly, Old World monkeys (which make up the majority of primates in laboratories) are more sociable than is sometimes acknowledged. Unlike the human species, their lives are constantly focused on a single group at any point in life, from birth to death. Human primates are simultaneously members of a variety of groups throughout life. My conclusion is that any primate housed alone is socially deprived. The stress from such deprivation is likely to distort both physiological (e.g., corticosteroid secretion) and behavioral (e.g., stereotypies) processes, even in adults previously reared in groups. Even more serious may be the effects of isolation on immature individuals.

Primate infancy and childhood are characterized by social stability (Figs. 2, 3, 4). The primate infant is constantly in the company of its mother, and often of older sibs as well. In monogamous species, the father is also present. This period of social dependency is longer in many species than previously suspected, e.g., in chimpanzees, weaning does not occur until the fifth year (Clark, 1977) and the average birth interval is almost six years (Tutin, 1980). Juvenile chimpanzees as old as eight years of age may grieve to death as a result of being orphaned. Such effects are not confined to apes. Long-term studies of orphaned female Japanese monkeys (*Macaca fuscata*) show them to have reduced reproductive success later in life (Hasegawa and Hiraiwa, 1980). In captivity, separation of infants from their mothers and rearing in varying degrees of isolation are more extreme than orphaning in the wild, where the immature primate may be fostered by kin who assume the role of substitute caretakers. Such allomaternal behavior is widespread (Quiatt, 1980). Single-caged housing in captivity precludes this, and although human caretaking may be sufficient to ensure survival, it may be more distorting than rearing in isolation in terms of negative effects in later life (Riesen, 1971). Contrary to earlier optimistic reports, behavioral abnormalities such as sexual dysfunction often cannot be reversed by social therapy (Goy and Goldfoot, 1974). Similarly, cumulative data from breeding



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Figure 2 A young chimpanzee cradles her first-born infant as she suckles.

records show that females who did not experience maternal rearing in their infancies make poor mothers, if they can be impregnated at all. In orangutans the two effects combine to produce a virtual absence of births from second-generation, captive-born parents, whereas wild-born individuals are successful in captivity (Jones, 1977).

Primates emigrate. Contrary to early reports, all primates do not grow up, live and die in the same group; at least half the members of any primate grouping leave the natal group and join another, or sometimes several others in succession. In monogamous species such as marmosets, offspring of both sexes leave at adolescence. In most species living in groups composed of several males and several females, males emigrate at sexual maturity. Such emigration was noted as occasional in early field studies of populations living at artificially high densities (Boelkins and Wilson, 1972). Later studies under more natural conditions suggest that most (Japanese monkeys, Sugiyama, 1976) or all (olive baboons, *Papio anubis*, Packer, 1975) males of such species will emigrate. However, in other species it is the females which transfer between groups either temporarily or permanently, e.g., in chimpanzees (Pusey, 1980). The proximate cause for such movement is the urge to breed outside the natal group; the ultimate cause is presumably avoidance of inbreeding-depression, the effects of which are now established (Ralls et al., 1979). Such findings have important implications for primates in captivity: Groups left intact are likely to deteriorate as stresses accumulate over years. Social problems are likely to increase and fertility to decline; the time-scale of the process should be predictable from the life history of the species involved. In Callithricidae (marmo-

sets and tamarins) antagonism between parents and young will emerge after the latter are succeeded by one or two sets of younger siblings. Such older offspring will not breed if left in the natal group. Similarly, removal and introduction of individuals in other species should involve the appropriate sex at the appropriate time. To exchange females rather than males between captive breeding groups of rhesus monkeys, as was done for years in one well-known research facility in England, resulted in prolonged social stress and possibly in reduced fertility.

Primate social life is based on kinship (Figs. 5, 6). A major finding from field studies is that social ties go beyond the parent(s) and offspring. Not only are sibs (or half-sibs, as is more usual) important, but also grandparents, uncles and aunts, and cousins, nieces and nephews. In many species of monkeys, matrilineal lines of several generations form the enduring core of a troop's social structure. Throughout their lives, such related individuals focus their social behavior, e.g., grooming, on each other, and form coalitions in competition. The evolutionary basis for such relationships appears to lie in kin selection (Hamilton, 1964), and the nature of social interactions can be predicted from the degree of relatedness, that is, the extent to which genes are shared between individuals (Kurland, 1977). Conversely, such individuals avoid engaging in incestuous reproduction, i.e., in son-mother, father-daughter, or sibling mating). This has been especially well-documented in the chimpanzee (Pusey, 1980; Tutin, 1980), where females actively avoid being mated by their sons and brothers. It is likely to hold true for all forms: There are no recorded cases in which incest is typical of naturally-living groups of primates. The reasons for this are likely to be those which underlie the incest taboo in humans, i.e., deleterious effects of homozygous recessive genes (Seemanova, 1971). The ramifications of such findings for confined primates are obvious. All individuals, even adults, housed alone are subject to 'kin deprivation;' moreover, infants growing up with only the company of their mothers are socially impoverished. Such individuals cannot be expected to engage in interaction in later life which requires reciprocity, as in the case of adult male olive baboons that help each other in competition over estrous females (Packer, 1977). By the same token, primates forced by lack of alternatives to breed to close kin will be stressed, their reproductive success is likely to decline, and any resultant offspring are likely to be at risk.



Figure 3 Two adult female green monkeys (*Cercopithecus sabaues*) with their infants.



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Figure 4 A young chimpanzee maintains contact with his mother as he begins to turn his attention to the rest of the world.

Primates breed selectively. Recent field studies show that *no* species of primate whose reproductive behavior has been studied breeds randomly. Early accounts of promiscuity lacked long-term data on identifiable individuals, or confused some aspects of sexual behavior with reproduction, *i.e.*, with fertilization. Such selectivity in breeding is based ultimately on sexual selection as expressed in competition among males over females (*intrasexual* selection) and in female choice of mates exercised on the basis of this competition (*intersexual* selection). The evolutionary aspects of this are now well understood, being based on sex differences in parental investment and the breeding strategies which follow from this (Trivers, 1972). For example, recent findings show that in wild chimpanzees, a supposedly promiscuous species, although the vast majority of copulations are opportunistic, most of the conceptions occur during consortships (Tutin, 1979). These are temporary, monogamous bondings which require mutual consent. In some polygynous species, competition between males may take the extreme form of one male killing the infants fathered by another (Hrdy, 1979). Even in species with great sexual dimorphism in body size, such as baboons, in which males may seem to dominate social affairs, it is the females who determine their impregnators (Collins, in prep.).

These observations have numerous implications for primates in captivity. For a male living in a pair with a female, or in a harem-group with two or more females, the spur of male competition is missing. This is especially important for species whose mating strategies evolved in multi-female, multi-male troops, e.g., all macaques, most baboons, and chimpanzees. The result may be progressively lower motivation to breed. Such forms should be housed in facilities of adequate size to hold two or more males. Similarly, females living in such captive conditions are prevented from exercising their choice of the fittest males, and their mental and emotional health may decline, along with their motivation to breed. Lack of choice may lead to forced matings. Chimpanzees paired in captivity mate throughout the menstrual cycle, whereas wild chimpanzees confine their matings to periods of female estrus (Tutin, 1980). Such matings result from male intimidation, and primiparous chimpanzees in captivity conceive earlier than their wild counterparts and show high rates of infant mortality (Tutin, 1980). Institutions seeking successful breeding of primates are advised to mimic as closely as possible the natural conditions under which the two sexes play out their mating strategies.



Figure 5 Two adult green monkeys are groomed by their offspring.

In summary, each species of nonhuman primate has social tendencies which are a result of its evolutionary past, *i.e.*, of a particular set of selection pressures imposed by the environment which shaped its genome. [That such genetic inclinations exist is revealed in those fortuitous conditions in nature where two neighboring, closely related species hybridize, e.g., the zone of overlap between olive baboons and hamadryas baboons in Ethiopia (Nagel, 1973).] These social inclinations manifest themselves at all levels — in interactions, relationships, and social structure, to use Hinde's (1976) terminology. These form the basis of the social capabilities cited in the title of this paper.

Origins of Cognitive Capabilities

It will be obvious that as our knowledge of the social worlds of primates increases, our estimations of their socially cognitive abilities must increase proportionally. Discrimination in interactions requires the ability to make judgments and distinctions; reciprocity in coalitions requires a memory with 'files' for individuals; competition over mates requires assessment of probabilities of relative success and

even costlier failures. Recent studies of primates do not shrink from using such terms as 'tactics' or 'strategies' to describe these abilities. De Waal (1978) has described the complex, conditional decision-making used by adult male chimpanzees in their alliance in dominance interactions. Walker Leonard (1979) has identified several alternative long-term strategies for stump-tailed macaques (*Macaca arctoides*), again related to eventual ranking in a dominance hierarchy. Wu *et al.* (1980) have shown that infant macaques have the ability to recognize half-sibs, even when they have been reared apart. (In all such cases, it must be emphasized that this need not entail conscious intent, but only that primates behave as *if* they were aware of the contingencies of behavioral alternatives.)

The plausibility of this social explanation for the evolution of intelligence should not blind us to other possibilities, however. More basic to evolution than reproductive success is individual survival. That is, in terms of inclusive fitness, an individual may advance its genes in the absence of reproduction by aiding its relatives, but an individual unable to stay alive becomes an evolutionary dead end. Primates as an order are the most varied and catholic of all mammals in diet. Much of their success in this regard derives from their skill at extractive foraging (Parker and Gibson, 1977). This entails exploiting resources which are not directly harvest-

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Figure 6 A juvenile female chimpanzee embraces her younger brother while their mother grooms herself.

able but which present 'detour' problems to be solved before eating. These challenges may take the form of an underground root or social insect colony, a tough-shelled fruit or skull, water in a tree-hole, or fungi under a stone (Hamilton et al., 1978; Rhine and Westlund, 1978). All of these tasks involve the indirect expenditure of energy, i.e., manipulation of objects other than the foodstuff before it can be eaten. Other species practice extractive foraging, e.g., squirrels with nuts, sea otters with abalones, but only in a limited and stereotyped way compared to the opportunistic, omnivorous monkeys and apes.

These recent findings on the cognitive aspects of feeding (which could easily be extended to the cognitive aspects of foraging, e.g., cognitive maps in wide-ranging species) reinforce a well-known point: Captive primates kept in bare cages without access to a continually changing array of manipulable objects are sensorially, motorically, and intellectually deprived. If their diet consists largely or entirely of artificial biscuits, the problem is compounded. Such nonhuman primates, no less than human ones, suffer pathogenic boredom, which shows in hair-pulling, coprophagy, and self-mutilation. This is especially regrettable when solutions exist: Chamove and Anderson (1980) have shown the beneficial effects of a deep litter substrate salted with small cereal grains, a technique which is both efficient and economical in providing opportunities for foraging.

Results from recent field studies of nonhuman primates continue to increase our estimation of their intelligence. This is the case whether we interpret its function in terms of the social demands of group-living or in terms of the environmental demands of individual subsistence. In either case (or more likely, with both acting together) the implications are clear. Primates in captivity that are socially or intellectually deprived are not realizing their evolutionary potential. Their behavior is abnormal in proportion to the degree to which such deprivation exists. Conclusions based on this abnormal behavior are suspect at best, and invalid at worst. Surely it is not beyond the ingenuity of users of primates in captivity to overcome these problems, as they have successfully done with so many others, to the mutual benefit of the human and nonhuman primates involved.

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