PART FIVE

Behavior

INTRODUCTION

KATERINA V. THOMPSON

For zoos to achieve their full potential in conservation and education, ensuring the mere survival of zoo specimens is not sufficient. We must also strive to preserve behavioral diversity among the animals in our care. If captive animals fail to exhibit normal reproductive and parental behavior, then captive propagation efforts will be futile; if animals fail to develop normal behavioral repertoires, then reintroduction attempts are doomed. Preserving behavioral diversity is a challenge for zoo managers, since the captive environment differs, in ways both obvious and subtle, from the habitats in which wild mammals evolved. This section provides a theoretical overview of aspects of behavior that have particular relevance to maintaining wild mammals in captivity and discusses how behavioral diversity can be preserved.

There are few things more discomforting to a zoo visitor than watching an animal pace endlessly and fruitlessly. Despite the recent emphasis on designing naturalistic exhibits to promote behavioral well-being in captive animals, the captive environment can never fully duplicate the habitats of wild mammals. Carlstead reviews how behavior is influenced by various facets of the captive environment in chapter 31. She also discusses behavioral abnormalities that can arise in captivity and suggests approaches to minimize the negative effects of captivity on behavior.

Koontz and Roush provide an overview of animal communication in chapter 32 and explain how features of the captive environment can enhance or interfere with normal communication. They further provide insight on how animal communication signals can be exploited by animal caretakers and managers to improve animal husbandry.

Wild mammals display an astonishing diversity of social organizations, from solitary to highly gregarious. The social organization of a given species, and therefore an individual animal's tolerance of conspecifics, is somewhat flexible and is influenced by both the environment (e.g., food, space) and the social milieu (e.g., age and sex of conspecifics). Berger and Stevens describe the various types of mammalian social organizations in chapter 33 and discuss how knowledge of a species' typical social organization and mating system can be used to determine the size and composition of captive groups.

In chapter 34 Thompson reviews the general patterns of behavioral development in wild mammals so that captive managers can evaluate the progress of animals in their care. She also describes methods of recognizing and encouraging play behavior among captive mammals, both for enhancing the educational value of exhibits and for promoting the well-being of zoo animals.

Knowledge of dietary requirements (see part 2, Nutrition, this volume) is useless if animals fail to consume the diets they are offered. Wild animals differ greatly in the methods they use to seek and consume food and in their willingness to experiment with unfamiliar food types. In chapter 35 Fernandes provides an overview of foraging behavior in mammals, with special emphasis on aspects that are immediately relevant to captive husbandry.

Future conservation efforts will combine in situ and ex situ activities. It has already been shown that behavioral deficiencies exist in zoo mammals that result in reduced survivorship when they are reintroduced into the wild. It is hoped that careful attention to behavioral needs will permit the expression of more normal behavior by individuals bred for reintroduction programs, and thus a more rapid adaptation to the wild and improved survivorship.

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Effects of Captivity on the Behavior of Wild Mammals

KATHY CARLSTEAD

The behavior of any species of wild mammal is the product of many generations of natural selection and adaptation to specific environmental conditions. Some species' behavior has evolved for the exploitation of very specific habitats, food resources, or climatic conditions, while other species have evolved the ability to adapt their behavior to various conditions depending on the seasonal, social, or biological factors predominating at any given time. Captivity, however, imposes on wild mammals an environment that may differ vastly from that in which they have evolved. To thrive under captive conditions, a species must accommodate to these differences. A species' ability to respond to captive conditions with behavior from its normal repertoire depends on a complex interaction of developmental, experiential, and genetic factors, as well as on the degree to which the particular captive conditions resemble its natural environment. The short-term success individuals have in coping with captive conditions affects their ability to breed in captivity; this initial success therefore affects the species' ultimate ability to exist as a captive population.

An animal's daily life is affected by physical and biological factors such as social and spatial restrictions, the presence of other species, including humans, and the availability of appropriate stimuli for the development and expression of natural appetitive, defensive, and protective behaviors. Such factors vary considerably across environments depending on the degree of "captiveness" or "wildness." However, the concept of "wild" versus "captive" is a false dichotomy. Populations of animals are found ranging freely in a wide variety of habitats, from "wild" reserves to semiwild sites where animals are provisioned. Populations termed "captive" inhabit sites ranging from large breeding corrals to complex zoo enclosures to single cages in laboratories. For simplicity, I will use "wild" and "captive" in this chapter to distinguish conditions tending more toward either extreme.

The chapter is divided into three major sections reflecting various levels of influence captivity may have on behavior: on the genetics of a captive population, on the development of behavior, and on the psychology of confined mammals. Reproduction in captivity may produce genetic changes in a captive population that distinguish it from wild populations. This would be of no consequence if captive mammal collections had constant access to new, wild-caught stock, but most zoos and propagation centers at present largely contain animals born and bred in captivity. Particularly if the desired end result is the preservation of an endangered species in a wild state, the long-term effects of captivity on behavior are important considerations (Kleiman 1980). A species' behavior derives from its genetic endowment, and because the long-term effects of captivity may act on gene frequencies in populations of captive mammals, I will begin this chapter on this theme.

LONG-TERM EFFECTS OF CAPTIVITY ON BEHAVIOR AND GENETICS

Captive populations are influenced by several random and nonrandom genetic mechanisms that may distinguish them from wild populations after a number of generations. Genetic variability is randomly reduced by inbreeding and genetic drift in small, relatively closed populations. Inbreeding increases homozygosity and may result in a lowering of fitness brought about by the expression of deleterious genes previously masked by dominant alleles. Ralls, Brugger, and Ballou (1979) present data indicating that mortality during the first 6 months of life is higher for inbred young of a number of zoo ungulate species than for noninbred young; the same has been reported for other inbred captive species (red panda, *Ailurus fulgens:* Roberts 1982; Przewalski's horse, *Equus przewalskii:* Bouwman 1977; eland, *Taurotragus oryx:* Treus and Lobanov 1971; leopard, *Panthera pardus:* Shoemaker 1982). Genetic drift, on the other hand, causes certain genes of neutral selective value to become "fixed" in a population as a result of their relative abundance in the small founding population.

Three primary selective mechanisms influence the gene frequencies of captive populations nonrandomly: artificial selection, natural selection, and relaxation of selection (Price 1984).

1. *Artificial selection* is selection for biological traits desired by humans. Such selection is goal-oriented and relatively fast when compared with the rate of change produced by natural selection in a wild population. Domesticated species have been selectively bred for biological traits of economic importance or for exaggerated morphological characteristics. Specific behavioral traits have been consciously selected in a few species, such as fighting cocks and guard dogs, but behavioral changes in domesticated populations have more often been the indirect consequence of selection for other, morphological attributes (Keeler 1975).
2. *Natural selection in captivity.* In the absence of interference by humans, the individuals possessing the phenotypes best able to adapt to captive conditions will have the highest reproductive success. This process of natural selection will be most intense in the first few generations after the transition from wild to captive environments (Price 1984).
3. *Relaxation of selection* can occur when captive conditions permit certain behavioral traits to remain in the population that would have been selected against under wild conditions. The result is an increase in genotypic and phenotypic variability for traits affecting behaviors such as food and shelter seeking, predator avoidance, and behaviors that serve to isolate populations reproductively.

Are zoo populations becoming domesticated? If the goal of zoos is to maintain wild animals in their most natural and original condition, zoo animals should not be managed like domestic animals (Hediger 1964, 1970). Price (1984) defines domestication as "that process by which a population of animals becomes adapted to man and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation." Humans have domesticated relatively few species, mostly out of economic need, and have domesticated mainly species predisposed to domestication by their social organization and reproductive behavior. Easily domesticated species generally live in large, hierarchical social groups in which the males affiliate with female groups, mating is promiscuous, and the young experience a sensitive imprinting period during development and are precocial. They are also generally adapted to a wide range of environments and dietary habits rather than to highly specialized conditions (Hale 1969; Clutton-Brock 1976). These characteristics permit easy control by humans. The mammal species found in zoological parks can be expected to be differently predisposed to domestication, and they probably differ greatly with respect to the adaptive behavioral changes that have already occurred, or may yet occur, as a result of generations in captivity. Purposeful selection for tameness or adaptation to captivity may be acceptable in cases in which the species is common in the wild and is kept in zoos only for display, or in the initial stages of establishing a captive population of a rare species that is not yet capable of self-sustaining reproduction in captivity (Frankham et al. 1986). Nevertheless, unconscious artificial selection for traits such as docility and tractability is probably occurring in zoo animals, selection that may eventually make captive populations genotypically divergent from wild populations.

Does wild behavior degenerate in captivity? Captive breeding of endangered species has been criticized because of concerns about the possible loss of wild behavior and the turning of animals into "degenerates" that cannot survive in the wild, as is said of many domesticated species (Hediger 1968; Bendiner 1981). However, it is highly questionable whether such long-term processes will have significant effects on the species-typical behavior of captive mammals. The stability of behavior patterns is generally underestimated, and in spite of numerous reports of behavioral differences between wild and domestic species, there is little or no evidence that domestication has caused behaviors to be eliminated from a species' repertoire (Hale 1969). Locomotor components of behavior, as well as the associated sensory capacities, tend to be so evolutionarily stable that behavioral criteria are even sometimes employed taxonomically to distinguish genera or species (Mayr 1958). Even among canids, for which there are extensive comparisons of wild and domestic behavior, no behavioral traits have been observed in domestic dogs that are not observed in their wild counterparts, except for tail carriage (Scott 1954). It would appear highly unlikely that any changes in normal species-typical behaviors would have evolved in zoo mammal populations since they have not undergone the extensive artificial selection of the domestic dog.

The main behavioral differences between captive and wild populations, therefore, are quantitative rather than qualitative. They are results of changes in intensity or releasing threshold, and may be brought about by genetic changes in the population (as discussed above), by learned adjustments to the captive environment occurring during the animal's lifetime, or by the unique stimulus situations existing in captivity (Hale 1969; Price 1984). For example, reduced aggressiveness toward conspecifics and humans in laboratory rats has been shown to be largely the result of being reared in social groups in small, open cages (Price 1978; Barnett, Dickson, and Hocking 1979) rather than due to genetic differences, even after many generations of artificial selection and inbreeding. Also, the absence of certain key stimuli in the physical environment of captive animals can result in failure to express certain behavior patterns. The burrowing behavior of domestic albino rats was found to be indistinguishable from that of wild rats when they were housed in large outdoor pens; the albinos also showed a variety of other wild-type behaviors under these conditions (Boice 1977). The rarity of certain behavior patterns in the repertoire of a population may also be a consequence of selection for a particular developmental phase. In young Malamute pups, unrestrained aggression and the absence of some threat displays normally seen in adult wolves, *Canis lupus lycaon,* were concluded to be the result of selection for neoteny (retention of juvenile characteristics) rather than due to relaxation of natural selection for these behaviors (Frank and Frank 1982).

Most wild mammal species have been bred in captivity for relatively few generations, and the current long-term effects of captivity on behavior are probably minimal. To maintain captive breeding populations of animals that exhibit behavior as it evolved in the wild, conscious or unintentional selection must be minimized and an environment provided that consists of the appropriate stimuli for eliciting wild behavior. This requires a thorough knowledge of behavior in the wild state as well as consideration of environmental influences on the development of behavior.

EFFECTS OF CAPTIVITY ON BEHAVIORAL DEVELOPMENT

The dynamic, ongoing interaction between an organism and its surroundings throughout development actively implicates the environment in determining the structure and organization of the animal's response systems (Moltz 1965). Animals born and reared in captivity may, therefore, be behaviorally distinct from those born and reared in a wild environment. The extent of this difference will depend partially on the degree to which the captive environment provides the appropriate stimulation during development and partially on the phenotypic plasticity of the species, that is, the extent to which the genotype is capable of entering into different classes of relationship with the environment (Moltz 1965).

During development, periods of heightened sensitivity to certain environmental stimuli may exert lasting influences on physiology, anatomy, and behavior. These "sensitive periods" are due in part to internal changes and may occur during various developmental stages in the animal's life. What is learned during these periods serves to narrow the animal's social or object preferences to that which is familiar. The irreversibility of some early experiences, however, may have maladaptive consequences for adult behavior when the experience acquired as a result of captive rearing does not correspond sufficiently with that normally acquired in the wild.

Prenatal Experience

Interactions between the developing organism and its environment start prior to birth, for the hormonal state of the mother affects the uterine environment of the growing fetus. Various effects of stress experienced by mothers during pregnancy on the behavior of their offspring have been reported, including increases (Ader and Belfer 1962) or decreases (Thompson, Watson, and Charlsworth 1962) in emotionality in a novel environment (open field) and alterations of exploratory behavior (Archer and Blackman 1971) in rats, and reductions in attack and threat behavior in male offspring (Harvey and Chevins 1985) in mice. Behavioral dysfunctions have also been found among human children born to mothers who experienced emotional stress during pregnancy (Stott 1973). Early motor development in rat pups was retarded when the mother was experimentally stressed with flashing lights and noise on an unpredictable schedule three times per week throughout pregnancy (Fride and Weinstock 1984). Fride and Weinstock hypothesize that glucocorticoids, produced by the mother when stressed, cross the placental barrier and affect the embryonic brain. In particular, the cerebellum is affected during sensitive periods in development. Corticosterone secreted by the mother in response to stress may also interfere with fetal testosterone production, which is necessary during fetal and early neonatal periods for the later development of masculine sexual behavior (Money and Ehrhardt 1972). The male offspring of mother rats stressed daily in the last week of gestation showed reductions in attempted copulations and ejaculation responses as adults (Ward 1972). Such studies imply that in a zoo environment, potentially stressful disturbances of pregnant mammals, such as relocation, zoo visitors, changes in management practices, social tension, or removal from a stable social group, could affect the viability and later behavior of their offspring.

The Early Social Environment

The social environment in captivity, if it deviates sufficiently from the wild situation, may deprive the young animal of specific stimulation essential for the development of normal, species-typical behavior. In mammals, rearing by the mother provides the infant with specific stimulation necessary for the normal development of emotional regulation, social interaction, and complex goal-directed behaviors, in particular, maternal and sexual behaviors. Maternal deprivation studies have demonstrated the long-term regulatory influence the parent-infant relationship may have on adult behavior, although there is a hiatus, due to a lack of systematic study, in our understanding of the processes underlying this regulatory function (Hofer 1981).

Tactile contact with the mother in rats has the immediate effect of eliciting activity in the pups, but when frequently repeated it reduces emotional reactivity later in life (Levine 1966; Hofer 1981). For rat pups, tactile contact with the mother, even if she is anesthetized and does not suckle the pups, is sufficient for suppressing emotional responses to novel stimuli at age 12–20 days (Levine 1986; Stanton, Wallstrom, and Levine 1987). Deprivation of maternal licking when pups are young has also been shown to affect the timing of sexual behavior patterns in male rats when grown; intromissions were more slowly paced and the rats took longer to ejaculate (Moore 1984).

Stimulation of the vestibular system provided by a moving mother is also important for the developing infant. Rhesus monkey *(Macaca mulatta)* infants raised with inanimate surrogate mothers that were stationary developed the self-rocking behaviors that are characteristically seen in isolation-reared monkeys, and in autistic or severely retarded children, while those raised with surrogates moving on a swing did not (Mason and Berkson 1975). The monkeys with moving surrogates did, however, retain other stereotypic patterns such as self-clasping and finger sucking. At 4 to 5 years of age they were less emotionally aroused, more responsive to partners, and benefited more from socializing experiences with peers than did the monkeys with stationary surrogates. This experiment not only illustrates the importance of vestibular stimulation as a component of parental care, but also shows some of the self-correcting behavior that developing young may perform in order to provide themselves with the necessary stimulation.

One of the main reasons for hand-rearing infant mammals in captivity is the mother's failure to provide adequate care. The reasons for such failures are diverse. Parturition is undoubtedly a stressful event for an animal, and maternal behaviors such as nest building, suckling, and retrieving are very labile (see also Hutchins, Thomas, and Asa, chap. 41, this volume). Stressful environmental events during and after parturition may disrupt these behaviors and result in rejection or harming of the infants. Parturient females may need nesting material, concealment, social isolation, silence, or temperature regulation. Failure to meet their special needs may result in a disruption of maternal behavior. The rearing strategy of a species must be carefully considered before forced isolation, forced contact with the young, or close confinement is imposed on the mother (Eisenberg and Kleiman 1977). Finally, inbreeding may account for a rise in the frequency of abnormal maternal behavior in a population, as is suggested in the case of cub killing in captive leopards (Shoemaker 1982).

Deficient maternal behavior, and even injurious behavior toward the offspring, may also be due to a lack of prior social experience with infants. Female rat pups placed postnatally with their mothers in environments with odors from other mothers with pups, or reared in groups with a large number of siblings, show superior maternal behavior in terms of pup retrieval and nest building compared with pups reared without odors or with a small number of siblings (Moretto, Paclik, and Fleming 1986). Hand-reared rhesus macaques avoid contact with their infants and are hyperaggressive toward them when they themselves become mothers ("motherless mothers": Harlow et al. 1966). Suomi (1986) points out that when Harlow started his research with rhesus macaques in the 1950s, most zoos made decisions to hand-rear captive-born primates based on health, safety, and hygienic considerations. However, once hand-rearing starts, it can become a vicious circle, producing more and more animals incapable of caring properly for their young unless compensatory experience is provided. Harlow and colleagues subsequently discovered that females who displayed aberrant infant care with their firstborn offspring could become competent mothers with later-born offspring if they remained with their firstborns for more than a week (Harlow et al. 1966; Ruppenthal et al. 1976), or if they had been given early social experience with mother-reared peers (Suomi 1986). Captive female chimpanzees, *Pan troglodytes,* are better mothers when they have social experience with nonrelated infants or mothers with infants (Hannah and Brotman 1990).

Despite the importance of the mother postnatally, social contact with peers may produce even more profound effects on later social behavior. Social deprivation studies (for a review, see Mineka and Suomi 1978) demonstrate the debilitating outcome of social deprivation. Hand-reared rhesus macaques totally isolated from conspecifics during their first few months exhibit irreversibly disturbed behavior when placed in a social group. They typically sit in a hunched position, spend large parts of their day in repetitive stereotypic motor behaviors, and are hyperaggressive, directing explosive physical attacks against their own bodies or against other monkeys. Sexual behavior is also usually aberrant (Goldfoot 1977). Laboratory rats deprived of any social contact between 22 and 70 days of age were also observed to be hyperaggressive to others when placed in a stable social group, and exhibited aberrant self-directed behaviors such as tail-chasing and manipulating the tail with the forefeet (Day et al. 1982). The excessive aggressiveness of many hand-reared zoo animals toward humans (Hediger 1964) and conspecifics, as well as some cases of self-mutilation, are analagous to these laboratory experiments; the social isolation from peers that may accompany hand-rearing can have devastating effects.

Many of the behavioral effects of isolation rearing can be overcome by providing even limited access to peers during development (see also Watts and Meder, chap. 6, this volume). Behavioral deficiencies in isolation-reared rats can be prevented by providing short periods of daily contact with peers involving rough-and-tumble play (Einon, Morgan, and Kibbler 1978). In rhesus macaques, however, adult sexual behavior remains deficient in most animals reared under conditions of limited access to peers (Goldfoot 1977). Some researchers suggest that the behavioral effects of isolation rearing on monkeys and rats are attributable to play deprivation (Einon, Morgan, and Kibbler 1978; Einon et al. 1981; Sackett 1974). Sackett theorizes that the hyperaggressiveness of isolation-reared rhesus macaques when placed in a stable social group is due to their failure to inhibit isolation-learned behaviors that are maladaptive in social settings. The function of play behavior may be to gain experience in the rapid alteration of roles and behavior patterns (Einon, Morgan, and Kibbler 1978). Isolation-reared juvenile rhesus macaques can be socially rehabilitated if they are allowed close physical contact with younger infants. The younger monkeys are less specific in their requirements for social interaction than are adults, and they provide the necessary interaction to socialize the isolates (Suomi and Harlow 1976). Hofer (1981) points out that there are many routes to the same developmental outcome in rehabilitation from the effects of aberrant early parenting; such compensatory schemes can and are being applied in zoos (i.e, in gorillas: Meder 1985).

Effects of Humans on Behavioral Development

One of the most distinctive elements of the captive environment is close contact with humans, a factor that can be expected to produce a range of behavioral characteristics not found in a wild-reared animal. Rearing in captivity may produce taming; Hediger (1964) defines tameness as "having no flight tendency with respect to man." Older wild-caught animals may be more difficult to tame than younger animals because of prior negative experience with humans or due to the absence of humans during the sensitive period for socialization. Older wild-caught moose, *Alces alces,* may never adapt to captivity and usually die of heart failure due to extreme tension (Hediger 1964).

The handling of young mother-reared mammals at an early age has been reported to have diverse effects on subsequent adult behavior, including speeding up the taming process. Generally, experiments in which mother-reared laboratory rat pups are handled at various stages of their early development produce adult animals that exhibit reduced emotional reactivity in a number of behavioral tests or in the presence of humans (Denenberg 1964, 1967). Enhanced learning in early-handled rats and primates has also been reported (Weiner et al. 1985). However, handling of young animals may also have detrimental effects, particularly if the stress of handling either the mother or the young interferes with the mother-infant relationship.

Close contact with humans at an early age, especially if it is in lieu of caregiving by the natural mother (i.e., hand rearing), leads to socialization with humans that may or may not have later consequences. Among ungulates with precocial young, filial imprinting, in which the young learn to follow the mother rather than objects and individuals that do not resemble the mother, occurs within the first day or two of life (for a review see Bateson 1966). Characteristics of filial imprinting have also been demonstrated in guinea pigs, *Cavia porcellus* (Sluckin 1968; Hess 1973). If a young animal is removed from the mother during the sensitive period for filial imprinting, following responses may come to be elicited by human caregivers, as is commonly seen in sheep and goats, but has also been reported in the American bison, *Bison bison,* zebra, *Equus* spp., African buffalo, *Syncerus caffer,* mouflon, *Ovis musimon,* and vicuña, *Vicugna vicugna* (Hediger 1968). Sexual imprinting, which leads an adult animal to direct sexual behavior preferentially to individuals resembling those it encountered when young, generally occurs during a sensitive period arising later than the sensitive period for filial imprinting. Most demonstrations of sexual imprinting, however, have been in birds; the evidence in mammals is inconclusive (Immelmann 1972). Generally, in mammals, subtle aspects of the parent-infant or juvenile-peer relationship affect later sexual preferences and competence such that one speaks of an extended period of socialization occurring during infant and juvenile stages (Bateson 1978).

Development of Learning in Captivity

Captive environments may be considerably less complex than relatively unrestricted, dynamic wild environments. Some experiments report functional variations in brain anatomy as a result of rearing in environments of varying physical complexity. Rats reared in a so-called "enriched" environment, for example, have a higher cerebral cortex weight, increased numbers of glial cells, and increased dendritic branching in the visual cortex (cf. Greenough 1976; Rosenzweig and Bennett 1976; Stein, Finger, and Hart 1983; for a review see Uphouse 1980). Behaviorally, they exhibit higher motor activity and more exploration in a standard test situation. There may also be differences in emotionality, and rearing in a physically complex environment may enhance learning to respond to a novel situation (e.g., Riittinen et al. 1986). Theories explaining the behavioral effects of experience with complex environments center on the environment-dependent development of neurons in the central nervous system that function to shape the animal's ability to cope with multiple and varied environmental challenges (Uphouse 1980).

Mental processes may develop differently in captivity than in the wild as a result of lower environmental complexity. Cognitive psychologists contend that animals possess learning mechanisms designed to detect and store information about causal relationships (Dickinson 1980). These relationships generally consist of two kinds of associations between constituent events, in which one event potentially causes another event either to happen or not to happen. In the complex and variable rearing environment of the wild, an animal learns that it can predict modifications in its environment as a result of its performing certain behaviors; it learns through experience with response-contingent stimulation that it can exert control over its environment. Without such experience, it learns that its behavior does not modify its environment in a predictable manner, and thus it may fail to respond optimally to new situations arising during its lifetime.

Mason (1978) suggested that experience with response-contingent stimulation is the essence of the mother-infant relationship; the mother provides a young animal with its first opportunities to learn that its behavior has effects on the environment and that the events around it are amenable to control. Mason reared rhesus macaque infants with surrogate mothers of two types, inanimate (a toy hobby-horse on wheels) and animate (a living dog). When he tested them at age 4, he found that monkeys raised with inanimate mothers were deficient in problem solving, often failing to respond at all to the test situation, and spent less time looking at projected photographs in a novel stimulus test. They were also unable to differentiate reliably between three levels of complexity in the slides. Mason's hypothesis is that a moving, responding mother provides her infant with stimulation that sustains interaction; even a mechanical swinging surrogate mother provides unpredictable movements that require adjusted movements from the infant (Mason and Berkson 1975). Such movements permit a young animal to learn that it can manipulate incoming stimulation by adjusting its own behavior. Deprived of experience with response-contingent stimulation, the animal is denied a motive for controlling its environment when faced with novel stimuli or problem-solving situations (Lewis and Goldberg 1969, cited in Mason 1978). (As mentioned above, Sackett [1974] proposed a similar explanation for the role of rough-and-tumble play in behavioral development, and indeed, rough-and-tumble play was three times greater in the 4-year-old monkeys in Mason's study that had been raised with animate surrogates than in those raised with inanimate surrogates.)

In another experiment, one group of rats was reared in a contingent environment in which they could control changes in lighting and presentations of food and water with lever presses. A second, noncontingent group housed in identical cages could make lever presses, but changes in their lighting, food, and water were yoked to the lever presses made by the contingent group (Joffe, Rawson, and Mulick 1973). Both groups thus received equal amounts of reward, but the contingent group had control over its onset and the noncontingent group did not. At 60 days of age, the contingent group rats, when tested in a novel, large, bare arena, were more active and explored more than rats from the noncontingent group, and were less emotional (as indicated by the number of defecations). Similarly, rhesus macaques were reared in three different environments: (1) they could control access to rewards of food, water, and treats; (2) rewards were as in (1) but were delivered randomly; and

(3) there were no rewards (daily feedings were given). When tested between the ages of 6 and 10 months, the monkeys with control over rewards were bolder in the presence of a fear-provoking toy, were more eager to enter a novel room and explored it more, and adapted better to stressful separation from peers than the monkeys without control (Mineka and Henderson 1985). Thus, lack of early experience in controlling environmental events can produce an animal that later is less able to adapt to stressful events and less likely to investigate actively and learn about novel situations. Overmeier and Seligman (1967) termed this response interference "learned helplessness," a term that has stuck despite the running debate on the actual psychological mechanisms involved.

The above examples are extremely relevant to the captive environment. Many zoo animals grow up in situations devoid of physical and social contingencies that would permit them to learn that their behavior can influence the environment. This may not matter if an animal is kept in a barren cage with no stimulation, but in a situation requiring a normal, adaptive response—for example, if it is placed in a novel environment or confined with a mate or young—its deficient experience may ultimately cause social discord, reproductive failure, disease, or even death. Fortunately, the emotional, cognitive, and anatomical deficits caused by rearing in impoverished environments, while long-lasting, may be subject to at least partial improvement by the provision of "therapy" in an enriched environment (Warren, Zerweck, and Anthony 1982; Stein, Finger, and Hart 1983). This finding is of relevance for zoo environmental enrichment programs designed to increase the activity levels of exhibit animals.

SHORT-TERM EFFECTS OF CAPTIVITY ON THE BEHAVIOR OF MAMMALS

The remainder of this chapter will discuss behavior that can be considered a direct response to the prevailing day-to-day conditions in captive environments. An animal's response to its surroundings depends on its sensory capabilities, motivational state, and previous experience with the environment. Together, these factors influence the animal's perceptions of the relevance of a given environmental stimulus and its subsequent attentional and behavioral responses. Along the continuum from captive to wild conditions, animals may use increasingly different behavioral mechanisms to adapt to their environments.

Control over the Environment

The main difference between captive and wild environments lies in the differential availability of control. Some theoretical models of behavior emphasize (1) that the degree to which an animal is stimulated by an event or situation external to itself is a function of the discrepancy between its expectations of stimulation and the actual stimulation, and (2) that the goal of a behavioral response is to control the level of stimulatory input (Sokolov 1960; Salzen 1962, 1970; Archer 1976; O'Keefe and Nadel 1978; Inglis 1983; Wiepkema 1985). A free-living animal is able to control the amount of incoming stimulation by making regulatory behavioral adjustments. It can approach, explore, attack, chase, escape, avoid, or hide from stimuli it encounters until the stimulation is brought to an acceptable level or until its expectations of stimulation are met. It can control its microclimate by moving to shade or sun, to shelter or wind, and it can satisfy appetitive motivation by actively seeking food, shelter, or a mate.

In captivity, on the other hand, an animal has a limited capacity to alter the external stimulation to which it is exposed. Many relevant stimulatory events are simply imposed on schedules that cannot be self-determined. Behavioral temperature regulation is often impossible, and appetitive motivation may have no appropriate outlet. Under these circumstances, the animal may be able to exert control over incoming stimulation only by modifying its expectations of its environment, as will be discussed below.

Evidence for the importance to developmentally nondeprived adult animals of being able to control their environment comes from experiments in which a choice is given between performing an active behavioral response to produce a biologically relevant event or having the event imposed. If rats are allowed to choose between receiving food that is delivered only upon performance of an operant behavior or receiving "free" food requiring no behavioral response, they overwhelmingly prefer to perform behavior for food (Singh 1970; review by Osborne 1977). Hungry rats trained to run down an alleyway to earn a pellet of food will even run past thousands of identical pellets to get to the goal box and obtain their reward (Stolz and Lott 1964; Overmeier, Patterson, and Weilkiewicz 1980). Deer mice, *Peromyscus maniculatus,* trained to operate levers controlling a motor-driven running wheel will run in it if they can start and stop it themselves, but they will not accept non-self-initiated motor-driven running (Kavanau 1963, 1964). Deer mice allowed to control illumination by lever presses will turn off a light each time it comes on automatically every half hour. If the light is automatically turned off every half hour, however, the mice turn it back on. Even though the mice have an aversion to bright lighting, having control over the illumination is sufficiently rewarding to override it.

The importance of behavioral control in adapting to *aversive* stimuli has also been demonstrated in many experiments, mainly with rats and mice. Weiss (1968) trained rats of one group to press a nose plate to turn off an electric shock administered to the tail. Rats of another group were "yoked" to the trained rats so that they simultaneously received the same shock as the first group, but they could not turn off the shock; it ceased only when the trained rat pressed the nose plate. Both groups thus received equal amounts of tail shock, but the trained rats had control over it and the yoked rats did not. The yoked rats eventually showed more severe physiological disturbances than the trained rats, including weight loss and gastric ulceration, indicative of severe stress. In other experiments, animals consistently able to escape shock showed fewer stress-related physiological responses than animals receiving the same amount of inescapable shock (Davis et al. 1977; Dess et al. 1983).

Captive animals may perform behaviors that provide perceptions of control rather than actual control. Some abnormal behaviors commonly observed in captive mammals may be the result of emotional arousal that has no appropriate behavioral outlet and becomes redirected to other objects or individuals. Winkelstraeter (1960) describes excessive self-scratching among primates frustrated by the failure of zoo visitors to respond to their begging for food. Sudden explosions of aggressiveness among animals that have lived together in apparent harmony may also be redirected responses to other, uncontrollable situations (Morris 1964; Meyer-Holzapfel 1968). Copulations with inanimate objects (Morris 1966) or with inappropriate partners without the normal courtship behaviors (Meyer-Holzapfel 1968) may be redirected expressions of arousal caused by unrelated, uncontrollable factors in the environment. Copulatory behaviors in laboratory animals can sometimes be induced by electric shock, handling, or novelty, or by frustration (Antelman and Caggiula 1980).

Without natural behavioral outlets, captive animals may have to rely on a conservation-withdrawal pattern of response characterized behaviorally by inactivity and submission. This response may allow the animal to obtain predictive information about the situation and thus alter its expectations of the stimulation impinging upon it. Freezing or crouching is a common response to diffuse, inescapable aversive cues that may allow the animal to monitor its situation (Blanchard and Blanchard 1969) and make preparatory physiological adjustments, as in stress-induced analgesia (for discussion, see Abbott, Schoen, and Badia 1984). The importance of predictive information for coping with aversive stimuli has been elucidated in experiments in which laboratory animals are delivered signaled or unsignaled shocks. Animals prefer conditions in which the inescapable shocks are signaled in a reliable manner (Seligman and Meyer 1968, 1970; Badia et al. 1976; for reviews, see Abbott, Schoen, and Badia 1984; Weinberg and Levine 1980). Feedback information about the cessation of the aversive stimulus may also be important because it helps the animal distinguish "safe," shock-free periods from periods in which shock is imminent (Weinberg and Levine 1980; Levine 1983).

Stress in Captivity

Threatening or aversive stimulation is experienced in wild and captive conditions alike and evokes similar physiological responses. If an animal, wild or captive, cannot cope with this stimulation, it may experience "stress." Coping is an active psychological process that alters threatening or aversive environmental conditions having stress as a major component (Levine 1983). In the previous section, I pointed out that the low controllability characteristic of captive conditions may require coping styles that tend toward reducing uncertainty. In this section, I will discuss the concept of "stress," means of assessing stress in confined animals, and the behavioral effects of chronic stress.

There is no generally accepted definition of stress, and it has many components that are not understood. The term "stress" is commonly used to refer to daily troubles and anxieties such as those experienced by human commuters or executives. With regard to nonhuman mammals, the term often refers to some unknown or intangible entity responsible for an animal's failure to behave or reproduce normally.

"Stress" may refer to different physiological and behavioral mechanisms, depending on the context. The term may be applied to an animal's physiological responses to extreme heat or cold, the social behavior of overcrowded laboratory animals, decreased productivity in farm animals, or the causes of pathology in animals or humans (Dawkins 1980). One reason for confusion is that the concept of stress is circular; diverse environmental variables elicit nonspecific autonomic and neuroendocrine responses with different time courses, as well as different behavioral responses. These behavioral reactions alter aspects of the environmental stimulation that initiated the response, subsequently influencing physiological and behavioral reactions, and so on. Discussion of "stress" thus may refer to the eliciting variables, or "stressors," to the autonomic and endocrinological changes, to behavioral adaptation, or to longer-term biological effects.

Originally, the term "stress" was used by Selye (1936, 1950) to refer to a nonspecific syndrome of physiological responses to noxious agents such as cold, heat, or physical pain. Selye's "general adaptation syndrome" is divided into three general stages. First, an alarm or emergency reaction to a stressor occurs, involving an acute activation of the sympathetic nervous system and adrenal medulla, secreting catecholamines that enable the organism to mobilize its "fight-or-flight" response (Cannon 1935). The resistance phase follows, in which activation of the neuroendocrine system, specifically, the hypothalamic-pituitary-adrenal (HPA) axis, occurs. ACTH (adrenocorticotrophic hormone) is secreted by the pituitary, stimulating the release of glucocorticoids (i.e., cortisol, corticosterone) from the adrenal cortex. Glucocorticoids amplify and extend the metabolic effects of catecholamines and help provide the body with energy in the form of glucose. Other pituitary hormones may also be released (e.g., growth hormone, prolactin, thyroid-stimulating hormone, gonadotropins) that inhibit growth and suppress reproductive function. In the final stage of the syndrome, if adaptation to the stressor does not occur or the stressor is not removed, gastric ulceration may occur and the biological defense system may become exhausted, with sequelae such as atrophy of the thymus and lowered immunological function.

Although Selye (1936, 1950) conceptualized the stress syndrome as being nonspecific because he believed the same endocrine processes to be elicited by a wide variety of noxious agents, other neuroendocrine systems have been found to respond in patterns characteristic of each stressor (Moberg 1985a). Although Selye used stressors that represented a physical insult to the animal, such as injection of foreign substances, x-rays, heat, or mechanical trauma, subsequent research has shown that the primary characteristics of stressful stimuli eliciting endocrine responses are *psychological* in nature (Selye 1956, 1974; for reviews, see Mason 1971; Hennessy and Levine 1979; Levine 1985). Mason was the first to emphasize that the apparent nonspecificity of the endocrine response lies in the psychological variables associated with the application of a noxious physical stimulus. If emotional arousal is carefully avoided when administering a treatment such as heat, cold, fasting, or exercise, the HPA axis is not activated. For instance, suddenly raising the room temperature by 15°C will increase circulating serum corticosteroid levels in rhesus macaques, but raising the temperature 1°C per hour to 15°C above normal will not (Mason 1971).

Experiments of this type have demonstrated that the complex hormonal changes that occur in conscious individuals subjected to stressful situations depend on subjective emotional experience. Levine (1985) states that "the basic cognitive process involved in stimulation of the pituitary adrenal system is one of comparison." Stress, according to his conception, is the endocrine responses to the cognitive variables of novelty and uncertainty. Mildly novel or uncertain situations may not be sufficiently aversive to activate the HPA axis, but as the degree of novelty or uncertainty increases, so does the stress response. In one example, rats normally housed in metal cages were handled only, placed in an unfamiliar metal cage with new bedding, placed in an unfamiliar metal cage with no bedding, or placed in a novel plastic container. All treatments caused increases in plasma corticosteroids, but the increases were larger for those treatments that deviated more from normal conditions in the order described above (Hennessy et al. 1979). Thus, the physiological stress response is graded according to perceptions of environmental change.

Individuals of the same species, sex, and age may differ greatly in their responses to the same environmental stimulus. There appear to be at least two different patterns of response to a perceived aversive situation: (1) an active "fight-or-flight" pattern characterized by increased activity, increased sympathetic adrenal medullary activation, and related increases in cardiac output and arterial pressure; and (2) a more passive "conservation-withdrawal" pattern characterized by decreased environment-directed activities, increased adrenocortical activation, and suppressed reproductive function (Engel 1967; Henry and Stephens 1977; Koolhaas, Schuurman, and Fokkema 1985; Moberg 1985b; Suomi 1986). Any individual may exhibit both types of response patterns; the pattern more likely to occur is dependent on rearing experience (Moberg 1985a) and genetic background (Gentsch, Vichtsteiner, and Feer 1981; Mormede et al. 1984; Suomi 1986). The idiosyncratic nature of stress responses is attributed to differences in perceptions of controllability and predictability (Dantzer and Mormede 1983; Levine 1985). There are complex interactions between the controllability and predictability components of coping responses (for reviews see Overmeier, Patterson, and Weilkiewicz 1980; Mineka and Henderson 1985). The effectiveness of predictive information in coping with aversive stimuli may be modulated by control over the situation (Davis and Levine 1982), or there may be preferences for predictability depending on the type of stressor (Badia, Harsh, and Abbott 1979; Davis and McIntire 1969). Animals thus have the capacity to develop individualistic coping styles based on their experiences with aversive stimulation, as humans are known to do (Miller 1980).

We can expect the behavioral responses of individual wild mammals in captivity to aversive stimuli to be diverse, idiosyncratic, and situation-specific. An animal crouching in the corner of its cage upon being approached may be experiencing considerably more adrenocortical activation than one that is actively bounding from wall to wall in the same situation (Duncan and Filshie 1980). When young squirrel monkeys, *Saimiri sciureus,* are separated from their mothers and placed in a novel environment, they exhibit signs of distress, such as heightened vocalization and activity, and increased plasma cortisol levels. If they are placed in a familiar environment with conspecifics when separated from their mothers, very few signs of distress are observed, but plasma cortisol levels are still very high (Levine 1983). In domestic pigs housed under five different conditions, Barnett et al. (1984) measured corticosteroid levels and recorded a number of agonistic, displacement, exploratory, manipulative, and resting behaviors. They found that only elevated frequencies of lying alone were correlated with elevated plasma corticosteroid levels. These examples demonstrate that no single behavioral variable adequately describes the response of an animal to a stressor in the environment.

It is extremely important to the health, reproduction, and welfare of an animal that it be able to inhibit or terminate adrenocortical activation. The physiological response to acute environmental change is usually of short duration. However, persistently recurring environmental events that an animal perceives as aversive and that it is unable to control or predict, or protracted aversive events such as separation, loss of attachment, or close confinement, may result in chronic elevations of adrenal hormones (Kant, Anderson, and Mougey 1987; Reichlin 1987; Rose 1987; Carlstead, Brown, and Strawn 1993) or produce adrenal hypersensitivity to ACTH (Armario et al. 1986; Friend, Dellmeier, and Gbur 1985; Mason, Brady, and Tolliver 1968; Restrepo and Armario 1987). "Chronic stress" is known to have a wide variety of deleterious, potentially fatal physiological and immunological consequences. Heightened glucocorticoid levels resulting from chronic stress result in interference with the action of insulin, loss of calcium from the bones and subsequent osteoporosis, suppression of growth, and contribution to the development of peptic ulcers. Chronically elevated steroid levels also suppress immune function by causing a reduction in T cell–mediated immune events and phagocytic function (Kelley 1985). Chronic stress may also suppress reproductive function (Eberhardt, Keverne, and Meller 1980; Moberg 1985b; Rideout et al. 1985).

One of the most obvious chronic stressors for a confined wild animal is the inability to respond to fearful situations with active avoidance or escape responses. Because most zoo animals have limited freedom of movement compared with their wild counterparts, they are often unable to withdraw effectively from aversive stimulation, whether caused by people or by cohabiting conspecifics. Siberian tigers, *Panthera tigris altaica,* at the Bucharest Zoo have been reported to develop gastroenteritis due to failing to adapt to unfamiliar quarters. A persistent high noise level lasting several months, caused by repairs in an adjacent courtyard, was also sufficient to induce gastroenteritis in some tigers (Cociu et al. 1974). The presence of zoo visitors may be underestimated as a chronic stressor for some mammalian species. Glatston et al. (1984) and Chamove, Hosey, and Schaetzel (1988) found clearly deleterious effects on the behavior of various primate species exposed to zoo visitors. Hediger (1964) describes situations in which captive animals have injured themselves or failed to breed because of their inability to escape from caretakers or visitors. He points out that the quality of the space provided for an animal may be more important for coping with escape-inducing stimulation than the quantity of space, because an animal may only need to perceive that it can retreat to safety rather than actually withdrawing (Bendiner 1981; Hediger 1964). Persistent auditory stimuli that vary in intensity, frequency, and content may be common stressors for captive animals (Stoskopf 1983). Chronic uncertainty about the actions of caretakers, workers, or veterinarians may also contribute to stress if the animal has no reliable predictive cues.

Chronic stress may lead to depression and lethargy in captive animals, as it does in humans. Fattening pigs housed in barren, overcrowded conditions often sit lethargically for long periods in a head-hanging position ("dog-sitting": van Putten 1980) and are unresponsive to their surroundings. In nonhuman primates separated from their mothers, depressive symptoms such as decreased play, decreased motor activity, severe loss of appetite, and sleep disturbances have been reported (Harlow and Zimmerman 1959; Harlow and Harlow 1965). These same symptoms can be induced in a variety of species by loss or separation from peers or mates, or by placement in an unfamiliar environment (Jesberger and Richardson 1985). Crawley (1984) observed increases in body weight and decreased social interaction and exploratory behavior in male Siberian dwarf hamsters, *Phodopus sungorus pallas,* separated from their mates for 3 weeks.

Stereotypies

A "stereotypy" is any movement pattern that (1) is performed repeatedly, (2) is relatively invariant in form, and (3) has no apparent function or goal (Odberg 1978). Stereotypies are common in zoo animals (Boorer 1972) but are rarely observed in wild, free-ranging animals. They occur in many species and have a wide variety of origins and proximate causes (see Mason 1991a for a review). Some stereotypic behaviors in zoo and farm animals occur when the animal consistently is unable to reach a particular goal by performing an appetitive behavior (Holzapfel 1938, 1939; Cronin 1985). For example, in many captive species, stereotypies occur mainly prior to feeding time, when the animal is motivated to perform food acquisition behaviors such as foraging or hunting. Winkelstraeter (1960) describes a female ocelot, *Felis pardalis,* that ran in a circular path prior to feeding. Geoffroy's cats, *Felis geoffroyi,* (K. Carlstead, unpub.) and an American black bear, *Ursus americanus,* paced for 2–4 hours before feeding time (Carlstead, Seidensticker, and Baldwin 1991). Stereotypies in ranch mink, *Mustela vison,* also peak in the hour before feeding time (K. Carlstead, pers. obs.). In tethered sows, the stereotypic movement pattern performed prior to feeding may have elements of thwarted feeding behaviors (Rushen 1984).

Physical thwarting of attempts to reach a desired place, animal, or object creates a similar appetitive situation that may cause stereotypy. A coati, *Nasua nasua,* that was locked out on exhibit away from her warm sleeping place would run back and forth repetitively for hours in front of the door to the den area (Meyer-Holzapfel 1968). Being separated from the rest of its pack resulted in a dingo, *Canis familiaris dingo,* pacing in a figure eight along a separating trellis (Meyer-Holzapfel 1968).

The inability to escape from a source of disturbance also contributes to stereotypy performance. A black bear, *Ursus americanus,* unable to withdraw from domineering conspecifics, was observed to "take little stereotyped walks" along a back wall as far away from the source of disturbance as possible (Meyer-Holzapfel 1968). Some fennec foxes, *Vulpes (=Fennecus) zerda,* ran repetitively back and forth for up to an hour after being disturbed by cage cleaning (Carlstead 1991), as did a female brown hyena, *Hyaena brunnea,* when zoo visitors were allowed too close to the cage front (Inhelder 1955).

Are stereotypies indicators of chronic stress? Stereotypic behavior in confined animals has long been considered an indication of poor welfare (e.g., Wiepkema 1983a; Broom 1983). This is because stereotypies often develop in situations known from independent behavioral and physiological evidence to be aversive and stressful, such as low stimulus input, physical restraint, or inescapable fear or frustration (Mason 1991b). Some researchers consider stereotypies to be a behavioral means of coping with a past or present aversive situation. Indeed, studies of the short-term effects of stereotypies have shown that high arousal is associated with the onset and development of stereotypies. Stereotypies seem to originate in behaviors that represent attempts by the animal to control its environment, such as escape attempts, aggressive acts against caging, and patrolling a territory (Holzapfel 1938; Cronin and Wiepkema 1985). As these actions fail to alter the animal's environment, the animal starts to organize a reduced number of behaviors into sequences that become rigidified, speeded up, repeated, and internally guided (Cronin and Wiepkema 1985; Morris 1966; Fentress 1976). However, evidence that the performance of stereotypic behavior reduces the level of stress or aversion experienced is equivocal (Rushen 1993; reviewed by Mason 1991a), suggesting that not all stereotypies may be a response to stress or aversion. In addition, individual coping styles play an important role in the expression of stereotypy in a given environment. This means that when individuals of the same species are compared, the degree of stereotypy may not necessarily reflect poorer or better welfare (Mason 1991b).

Stereotypies are sometimes thought to be caused mainly by space limitations. It is generally true that the smaller the cage, the more likely an animal is to perform a stereotypy (Paulk, Dienske, and Ribbens 1977). By increasing the size of the area available to an animal, the behavior can sometimes be eliminated or altered (Draper and Bernstein 1963; Clarke, Juno, and Maple 1982). Certainly the size and shape of an animal's cage play a role in shaping the stereotypic motor pattern an animal performs. In few cases, however, is it clear exactly how much space is needed to ensure the absence of stereotypies (Stevenson 1983). Indeed, there is evidence that cage size in some cases is not the critical factor (Berkson, Mason, and Saxon 1963). Odberg (1987) compared the behavior of voles, *Clethrionomys glareolus*, in small, rich environments and in large, sparse ones, and found less stereotypic jumping in the former. Sows kept tethered in stalls will perform considerably fewer stereotypies in the same space if they are given a handful of straw to manipulate (Fraser 1975). An American black bear virtually ceased to pace in its exhibit when provided with opportunities to forage for food (Carlstead, Seidensticker, and Baldwin 1991). Such evidence, combined with the observation that most stereotypies occur in situations in which an appetitive action fails to produce a desired endpoint, lends credence to Hediger's (1964) statements that the quality of a confined animal's space is more important than the quantity.

Stereotypies are clearly an indication of an abnormal animal-environment interaction. For most wild mammals in captivity, this probably means that the animal grew up in or is currently living in an environment suboptimal for meeting its natural, species-specific behavioral needs. Hediger (1934, 1938) long ago pointed out that we can better understand the needs of captive animals by studying their stereotypic motor reactions. Thorough studies of the development of stereotypic behavior are needed to help elucidate the deficiencies of the environments we impose on captive wild mammals.

Behavioral Effects of Low Stimulus Diversity

The term "boredom" is often used to describe the way confined mammals experience their undiversified world. Boredom is the psychological response to an environment that fails to meet the animal's needs for stimulation due to low stimulus diversity.

An animal's "needs" for stimulation are difficult both to define and to quantify. These needs are subject to great individual and species variability (Dawkins 1980). Although novelty and uncertainty may be aversive at times, not all novel or uncertain stimulation is negative. Many people experience mild stress as pleasant or as putting them in a productive state. People also seek the elevated levels of stimulation provided by the unusual or unexpected for brief periods in order to amuse themselves or when feeling bored. Certainly much of the arts and entertainment industry depends on this fact (Hebb 1949). Animals too perform exploratory, appetitive, and play behaviors that allow them to encounter novel or unexpected objects or situations, and they investigate novel stimuli presented in familiar surroundings (Glickman and Scroges 1966). In laboratory experiments giving rats a choice between novel and familiar environments, the rats, under normal circumstances, choose the novel (Hughes 1968; Montgomery 1953), and they will learn operant tasks to produce a variety of stimulus changes (for a review see Kish 1966). Animals and people therefore seem to seek changes in stimulation in similar circumstances.

In an environment low in stimulus diversity, an animal will find it difficult to exert control over the stimulation to which it is exposed. As with aversive stimuli, there may be two ways of adapting to low stimulus diversity: one response is to keep on performing the behavior necessary to find or create the desired stimulation; the alternative is to suppress or modify expectations of stimulation to fit what is available in the environment. Compared with the captive situation, appetitive and exploratory behaviors in the wild are far more likely to produce the expected stimulation; therefore, lowered expectations may be the prevailing response of animals in monotonous environments.

Chronically understimulating conditions in a captive environment may affect the behavior, psychological welfare, and health of wild mammals in two broad ways: (1) by causing decreases in stimulation-seeking behavior (lethargy), and (2) through the animals' attempts to increase stimulatory input by means of autostimulation or performance of appetitive or social behaviors in unnatural contexts.

Lethargy in confined mammals is characterized by relative inactivity and drowsiness. Animals confined in stimulus-poor, monotonous environments for prolonged periods are less likely to perform active stimulation-seeking behaviors when presented with the appropriate opportunity than are animals experienced with complex, contingent environments. I have already discussed the effects of impoverished environments on the development of normal levels of activity and emotionality in young animals. Effects of stimulatory impoverishment and enrichment have also been demonstrated in adult animals. Inglis (1975) raised rats in opaque plastic cages, then when they were adults placed half of them for 5 weeks in wire cages provided with activity wheels, toys that were changed daily, and changes in lighting and noise levels. The other rats were kept in their original plastic cages in constant dim lighting and quiet. The rats experiencing enriched conditions subsequently demonstrated an increased willingness to explore a novel maze and quicker habituation to novel surroundings. Butler (1957) deprived rhesus macaques of visual pattern stimulation for varying numbers of hours, then allowed them to seek access to visual stimulation. He found a decrease in stimulation-seeking behavior for deprivation periods longer than 4 hours.

This evidence implies that chronically understimulated captive animals depress their needs for stimulation by lowering their expectations of the level of stimulatory input from their surroundings. This also appears to be the case in humans. Experiments in which people are deprived of sensory stimulation for an extended period indicate that stimulation seeking declines and a preference develops for little or no change in environmental stimulation. Prison inmates isolated under conditions of perceptual deprivation for 7 days showed a lowered preference for high levels of visual input (Gendreau et al. 1968).

Animals chronically deprived of stimulus diversity may respond poorly when highly stimulating, novel situations arise; for example, they may overreact and fail to adapt to sudden changes, even to the point of death. Christian and Radcliffe (1952) reported on fourteen zoo animals that had been housed in small indoor cages and then died after being subjected to the acute stress of transfer to a new cage or disturbance by workers. In all these cases the adrenal cortex had atrophied, indicating an inability to sustain a response to the extreme stimulation and a failure to adapt to the new situation. Swine reared in impoverished intensive farming conditions often die during transport to the slaughterhouse due to the psychological trauma associated with the extreme change in surroundings and contact with unfamiliar pigs. Thus, chronic "boredom," although perhaps not stressful, can lead to hyperresponsiveness to stressors when they present themselves.

The second category of behavioral effects of boredom comprises attempts of animals to stimulate themselves in the face of an impoverished environment. Many cases of abnormal self-directed behaviors, such as the self-rocking and digit sucking mentioned previously in isolation-reared monkeys, have been explained as attempts by a sensorily deprived animal to stimulate its own nervous system. Other self-directed behaviors common in primates are visual fixation on or slapping of a part of the body (Paulk, Dienske, and Ribbens 1977), huddling combined with hopping or walking, rolling in a ball, and vertical circling about the cage (looping). Autostimulation is common in primates deprived of tactile stimulation during development (for a review see Mitchell 1970), but has also been observed in other mammals reared in isolation (Morris 1964; Erwin and Deni 1979). Social animals that were not deprived during development may also exhibit abnormal self-directed behaviors when housed separately from groupmates (Morris 1964; Antelman and Caggiula 1980).

Autostimulation may develop into extreme forms of self-mutilation. Self-mutilation is reportedly most common in opossums, carnivores, long-tailed monkeys, and the small South American monkeys. Meyer-Holzapfel (1968) describes several cases in which entire paws or tails were gradually gnawed away, sometimes because there was initially an injury or irritation to the appendage. Ranch mink often have damaged tails in captivity (approximately 10–20% of all individuals), although this is rare in the wild. They develop tail-biting and sucking habits that persist through molting periods, and some have been observed to run in circles in their cages, chasing the tail and biting it (de Jonge, Carlstead, and Wiepkema 1986).

Coprophagy, the eating of fecal material, and regurgitation/reingestion are also considered to be self-stimulatory responses to the boredom of captivity, particularly in the great apes (Stevenson 1983). Sixty-nine percent of 117 captive gorillas, *Gorilla gorilla,* sampled engaged in regurgitation/reingestion behaviors (Gould and Bres 1986). Hand-reared individuals, whether wild-caught or captive-born, showed a higher incidence than mother-reared individuals. Gould and Bres had some success in reducing these behaviors by feeding browse, and concluded that the time spent handling and ingesting food in captivity is too low.

Animals may also increase stimulation by performing behaviors that are natural in form, but seemingly out of context, or performed in an excessive manner because of the unavailability of the appropriate environmental stimuli as a guide. For example, excessive licking, biting, and chewing of wood, bars, fences, or hair may occur in grazing animals that are fed concentrated pelleted diets (Hintz, Sedgewick, and Schryver 1976). Morris (1964) describes cases of various carnivores copulating with objects such as bedding material, feeding dishes, or a scratching post. Animals may also create behaviors that are "occupational" in nature; Morris (1964) provides several examples of innovative visitor-oriented and object-oriented behaviors that take the place of naturally occurring behaviors. Food begging in zoo animals that are well fed and need not beg out of hunger is an example of a substitute for foraging that is adapted to the captive environment (van Keulen-Kromhout 1978). Visitor-oriented behaviors such as object throwing by great apes and elephants and urine spraying by carnivores and primates are manipulative activities that elicit pronounced responses from the human recipients (Morris 1964). Cats that throw dead prey up in the air so that they can pounce on it and "kill" it, and canids and viverrids that shake a dead prey object "to death" before eating it, provide further examples of stimulation-increasing behaviors in captive mammals.

ENVIRONMENTAL ENRICHMENT

The behavior of an animal is the principal means by which zoo personnel *and* zoo visitors assess its psychological welfare; the more its behavior resembles that of its wild counterparts, the more certain we are of an animal's general well-being. Animal exhibitors should strive for both a naturalistic setting and the performance of appropriate natural behaviors.

Providing occupation that gives confined animals some control over their environment is essential for their psychological welfare and for the display of ecologically valid behavior (Hediger 1968; Markowitz 1975). In general, "environmental enrichment" means providing a complex and diverse environment that increases the possibility that the captive animal's own behavior will produce what it needs: finding food, demarcating a territory, building a nest, maintaining its physical condition, escaping conspecifics, or hiding. An animal with more behavioral options will be better able to cope with stressful events in its surroundings or alleviate boredom. Behavioral options can be improved by increasing the complexity and variability of the environment physically, sensorily, and socially. Maple and Perkins (chap. 21, this volume) provide a review of some of the ways this can be accomplished with exhibit furnishings.

The spaces to which wild mammals are confined vary considerably in physical complexity. Behavioral improvements may be contingent upon specific components contained in the enclosure rather than larger size alone. Many zoos have found that larger, more natural-looking exhibits do not necessarily lead to greater activity or more normal behavior (Spinelli and Markowitz 1985). In a survey of gorilla and orangutan, *Pongo pygmaeus,* enclosures in forty-one zoos, Wilson (1982) found that the factors most highly correlated with activity levels were, for both species, the number of animals present; for gorillas, stationary and temporary objects available; and for orangs, stationary and movable objects available. The size and construction of the enclosure were not correlated with activity levels.

Certain behaviors may be affected more than others by increases in enclosure size and complexity. For example, moving four chimpanzees from laboratory cages to a large, naturalistic artificial island resulted in a drastic reduction in stereotypic and self-directed behaviors, but had no effect on social behaviors (Clarke, Juno, and Maple 1982).

Environmental complexity can be increased when space is limited by providing structures that increase the surface area over which an animal can move and that make use of the vertical space of a cage or enclosure. Methods of increasing sensory complexity also should not be overlooked; for example, spraying cologne on tree stumps and branches stimulates investigation and rubbing by wolves (K. Kranz, pers. comm.). Another manner of increasing environmental complexity is to supply the enclosure with objects the animal can manipulate. Beer kegs and oil drums have proven to be suitable toys for great apes (van Hooff 1973) as well as many other large species (bears, tigers), especially when they can be used in water. Their irregular shape and buoyancy produces unpredictable movements that can sustain the animal's attention for long periods. A swinging boxing bag hung in the enclosure of a rhinoceros will elicit hours of rubbing and butting because it "responds" to the animal's actions with unpredictable movements of its own. Hanging a large dead branch from a tree in elk and deer yards provides the bull with an engaging moving surface on which to scrape his antlers (Hancocks 1980; Hutchins, Hancocks, and Crockett 1984). However, zoo staff need to consider how the qualities of toys, such as manipulability, flexibility, predictability of movement, smell, and complexity, will appeal to the skills of a particular species. Also, habituation to toys should be reduced by removing them periodically, varying the objects presented, filling them with food snacks, or placing them in novel positions or locations (Carlstead, Seidensticker, and Baldwin 1991).

Keeping mammals in appropriate social groupings is an extremely important means of creating complex environments. Social partners are an infinite source of response-contingent stimulation, allowing an individual to interact with its surroundings to a much greater degree than if it were alone. Housing gorillas and other primates in large groups is a trend that radically departs from the past and has led to a large increase in the successful breeding and natural rearing of young (Beck and Power 1988; Maple and Finlay 1989).

One important means of enriching an animal's environment is to increase greatly the time spent in food acquisition. In the wild, many species spend most of their waking hours looking for, pursuing, gathering, handling, or hiding food. Gorillas, for example, spend up to 70% of their day foraging and feeding (Maple and Finlay 1987), and black bears, 75% (Garshelis and Pelton 1980). In the vast majority of captive situations, animals are fed in one or several daily meals by human caretakers. No effort is expended to acquire the food, and it is consumed in a short time. Environmental enrichment measures that direct activity toward foraging may have beneficial effects on behavior that are preferable to the effects of merely providing toys and manipulable objects. For example, cynomolgus monkeys, *Macaca fascicularis,* normally housed in bare cages were allowed to spend an hour each day in a "playpen" cage provided with toys, manipulable materials, visual access to the neighboring animal, and deep woodchip litter sown with sunflower seeds and peanuts. Their preferred activity during this hour was to forage for the food snacks (Bryant, Pupniak, and Iverson 1988).

Naturalistic methods of feeding involve presenting food so that the animal must search for and gather it or spend time handling it; for example, by scattering small food items mixed in with a substrate or in hay (e.g., grain or mealworms in woodchips or woodwool: Chamove et al. 1982). The behavior patterns required to retrieve food fed by naturalistic delivery methods are more varied, the places of finding food more random, and the time occupied longer than with traditional feeding methods or mechanical feeders. Feeding lion-tailed macaques, *Macaca silenus,* fruits and vegetables whole rather than chopped increases dietary diversity, time spent feeding, and total amount of food consumed (Smith, Lindburg, and Vehrencamp 1989). The effects of such feeding on other behaviors may be profound: for an American black bear, hiding food throughout the exhibit virtually eliminated stereotypic pacing, whereas feeding from a mechanical feeding device did not (Carlstead, Seidensticker, and Baldwin 1991).

CONCLUSIONS

One of the major premises of this chapter is that wild mammals reared in a captive situation adapt their behavior to their environment, no matter how impoverished or enriched. The behavioral options wild mammals have for responding to captive environments have been examined, and the potential costs in terms of behavioral abnormalities, lethargy, and compromised health and reproduction have been mentioned. However, another, more general, potential cost of keeping animals in confinement must be considered: animals that do not exhibit a wide range of natural behaviors give the impression to zoo visitors of being either bored and unhappy in their enclosures or tormented by their confinement. Under these circumstances visitors will fail to develop an appreciation of biological diversity and the need to conserve it. Although the aesthetics of "naturalistic" exhibits have greatly improved in recent years, most new enclosures still fail to accommodate the animal's natural behavior. This may have been acceptable in the past, but zoo visitors today are often well-informed of animal habits through wildlife television documentaries, and zoos run the risk of provoking disappointment if they cannot exhibit active, normally behaving animals.

To maintain wild-type behavior in captivity it is necessary to fit environmental conditions to the animal, rather than expecting the animal to adapt to the conditions we impose upon it. This can be accomplished only with a thorough knowledge of an animal's long- and short-term behavioral needs. In the long term, reduced genetic variability in captive populations may have consequences for behavioral traits, but this can be determined only by comparison with wild populations, and that is often difficult or impossible, especially for rare and endangered species. Most of the effects that captivity exerts on behavior occur in the short term to the individual animal as it grows up under the specific conditions of its confinement.

The immediate psychological goal of behavior for an animal is to control the stimulation impinging upon it from its surroundings. In most cases in the wild, the animal can take a behavioral action that will increase or decrease the intensity of events happening around it. Captive conditions, being more restrictive and less diversified than the wild, may offer the animal little opportunity for behavioral control. Mammals may adapt to these circumstances by adopting passive, inactive behavioral strategies geared toward uncertainty reduction as a means of controlling aversive stimulation, or by adopting decreased expectations of stimulation as a means of coping with boredom. The low stimulus diversity of the more impoverished captive environment may cause lethargy and inactivity, hyperresponsiveness to unusual or unexpected events, or an inability to cope with stress. In an inappropriate environment, high motivation to perform a certain type of behavior may lead to abnormal self-directed behaviors, behaviors performed in an unnatural context, stereotypy, or excessive aggression.

It *is* possible, however, to provide adequate captive environments for wild mammals if their specific needs are learned and taken into consideration when designing exhibits and husbandry procedures. Recent developments in zoo research, developmental psychobiology, and animal welfare science provide an optimistic outlook for the future management of wild mammals in captivity as breeding populations. Many things can be done to enrich the environment of captive mammals, and such strategies may improve behavior even to the point of rehabilitating previously severely deprived animals. Increasing the physical and social complexity of the environment provides the animal with more behavioral options for responding to stimulation from its surroundings and gives it more opportunities to create stimulus change by manipulating its own surroundings. One of the most obvious and direct means of doing this is to devise alternatives to the standard method of feeding captive mammals in large daily meals. The large amounts of time spent in food acquisition behaviors in the wild need to be directed in captivity so that these behaviors do not find their outlet in some other, inappropriate context. Further research into the specific behavioral needs of each mammal species is necessary in order to develop appropriate environmental design and husbandry in captivity.

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REFERENCES

Abbott, B., Schoen, L., and Badia, P. 1984. Predictable and unpredictable shock: Behavioural measures of aversion and physiological measures of stress. *Psychol. Bull.* 96:45–71.

Ader, R., and Belfer, M. 1962. Prenatal maternal anxiety and offspring emotionality in the rat. *Psychol. Rep.* 10:711–18.

Antelman, S. M., and Caggiula, A. R. 1980. Stress-induced behavior: Chemotherapy without drugs. In *The psychobiology of consciousness,* ed. J. M. Davidson and R. J. Davidson, 65–103. New York: Plenum Press.

Archer, J. 1976. The organization of aggression and fear in vertebrates. In *Perspectives in ethology,* vol. 2, ed. P. P. G. Bateson and P. Klopfer, 231–98. London: Plenum Press.

Archer, J., and Blackman, D. 1971. Prenatal psychological stress and offspring behavior in rats and mice. *Dev. Psychobiol.* 4: 193–248.

Armario, A., Lopez-Calderon, A., Jolin, T., and Balasch, J. 1986. Response of anterior pituitary hormones to chronic stress: The specificity of adaptation. *Neurosci. Biobehav. Rev.* 10:245–50.

Badia, P., Harsh, J., and Abbott, B. 1979. Choosing between predictable and unpredictable shock conditions: Data and theory. *Psychol. Bull.* 86:1107–31.

Badia, P., Harsh, J., Coker, C., and Abbott, B. 1976. Choice and the dependability of stimuli that predict shock and safety. *J. Exp. Anal. Behav.* 26:95–111.

Barnett, J. L., Cronin, G. M., Winfield, C. G., and Dewar, A. M. 1984. The welfare of adult pigs: The effects of 5 housing treatments on behavior, plasma corticosteroids, and injuries. *Appl. Anim. Behav. Sci.* 12:209–32.

Barnett, S. A., Dickson, R. G., and Hocking, W. E. 1979. Genotype and environment in the social interactions of wild and domestic Norway rats. *Aggressive Behav.* 5:105–19.

Bateson, P. P. G. 1966. The characteristics and context of imprinting. *Biol. Rev.* 41:177–220.

———. 1978. Early experience and sexual preference. In *Biological determinants of behaviour,* ed. J. B. Hutchinson, 29–53. London: Wiley.

Beck, B. B., and Power, M. L. 1988. Correlates of sexual and maternal competence in captive gorillas. *Zoo Biol.* 7:339–50.

Bendiner, R. 1981. *The fall of the wild, the rise of the zoo.* New York: E. P. Dutton.

Berkson, G., Mason, W. A., and Saxon, S. V. 1963. Situation and stimulus effects on stereotyped behaviors of chimpanzees. *J. Comp. Physiol. Psychol.* 56:786–92.

Blanchard, R. J., and Blanchard, D. C. 1969. Passive and active reactions to fear-eliciting stimuli. *J. Comp. Physiol. Psychol.* 68: 129–35.

Boice, R. 1977. Burrows of wild and domestic rats: Effects of domestication, outdoor raising, age, experience, and maternal state. *J. Comp. Physiol. Psychol.* 91:649–61.

Boorer, M. 1972. Some aspects of stereotyped patterns of movement exhibited by zoo animals. *Int. Zoo Yrbk.* 12:164–66.

Bouwman, J. 1977. The future of Prezwalski horses *Equus przewalskii* in captivity. *Int. Zoo Yrbk.* 17:62–67.

Broom, D. M. 1983. Stereotypies as animal welfare indicators. In *Indicators relevant to farm animal welfare,* ed. D. Schmidt, 81–87. Current Topics in Veterinary Medical Animal Science, 23. The Hague: Martinus Nijhoff.

Bryant, C. E., Pupniak, N. M. J., and Iverson, S. D. 1988. Effects of different environmental enrichment devices on cage stereotypies and autoaggression in captive cynomolgus monkeys. *J. Med. Primatol.* 17:257–69.

Butler, R. A. 1957. The effect of deprivation of visual incentives on visual exploration motivation in monkeys. *J. Comp. Physiol. Psychol.* 50:177–79.

Cannon, W. B. 1935. Stresses and strains of homeostasis. *Am. J. Med. Sci.* 189:1–12.

Carlstead, K. 1991. Fennec fox *(Fennecus zerda)* husbandry: Environmental conditions influencing stereotypic behavior. *Int. Zoo Yrbk.* 30:202–7.

Carlstead, K., Brown, J. L., Monfort, S. L., Killens, R., and Wildt, D. E. 1992. Urinary monitoring of adrenal responses to psychological stressors in domestic and non-domestic felids. *Zoo Biol.* 11:165–76.

Carlstead, K., Brown, J. L., and Strawn, W. 1993. Behavioral and physiological correlates of stress in laboratory cats. *Appl. Anim. Behav. Sci.* 38:143–58.

Carlstead, K., Seidensticker, J. C., and Baldwin, R. 1991. Environmental enrichment for zoo bears. *Zoo Biol.* 10:3–16.

Chamove, A. S., Anderson, J. R., Morgan-Jones, S. C., and Jones, S. P. 1982. Deep woodchip litter: Hygiene, feeding and behavioral enhancement in eight primate species. *Int. J. Stud. Anim. Prob.* 3 (4): 308–18.

Chamove, A. S., Hosey, G. R., and Schaetzel, P. 1988. Visitors excite primates in zoos. *Zoo Biol.* 7:359–69.

Christian, J. D., and Ratcliffe, H. L. 1952. Shock disease in captive wild animals. *Am. J. Pathol.* 28:725–37.

Clarke, A. S., Juno, C. J., and Maple, T. L. 1982. Behavioral effects of a change in the physical environment: A pilot study of captive chimpanzees. *Zoo Biol.* 1:371–80.

Clutton-Brock, J. 1976. The historical background to the domestication of animals. *Int. Zoo Yrbk.* 15:240–44.

Cociu, M., Wagner, G., Micu, N. E., and Mihaescu, G. 1974. Adaptational gastro-enteritis in Siberian tigers. *Int. Zoo Yrbk.* 14: 171–74.

Crawley, J. N. 1984. Evaluation of a proposed hamster separation model of depression. *Psychiatry Res.* 11:35–47.

Cronin, G. M. 1985. The development and significance of abnormal stereotyped behaviours in tethered sows. Ph.D thesis, Agricultural University of Wageningen, Netherlands.

Cronin, G. M., and Wiepkema, P. R. 1985. An analysis of stereotyped behaviour in tethered sows. *Annales Recherche Veterinaire* 15:263–70.

Dantzer, R., and Mormede, P. 1983. Stress in farm animals: A need for reevaluation. *J. Anim. Sci.* 57:6–18.

Davis, H., and Levine, S. 1982. Predictability, control, and the pituitary-adrenal response in rats. *J. Comp. Physiol. Psychol.* 96:393–404.

Davis, H., and McIntire, R. W. 1969. Conditioned suppression under positive, negative, and no contingency between conditioned and unconditioned stimuli. *J. Exp. Anal. Behav.* 12:633–40.

Davis, H., Porter, J. W., Livingstone, T., Hermann, T., MacFadden, L., and Levine, S. 1977. Pituitary-adrenal activity and lever-press shock escape behavior. *Physiol. Behav.* 5:280–84.

Dawkins, M. S. 1980. *Animal suffering: The science of animal welfare.* London: Chapman and Hall.

Day, H. D., Seay, B. M., Hale, P., and Hendricks, D. 1982. Early social deprivation and the ontogeny of unrestricted social behavior in the laboratory rat. *Dev. Psychobiol.* 15:47–59.

de Jonge, G., Carlstead, K., and Wiepkema, P. R. 1986. *The welfare of ranch mink.* Publication 010, Centre for Poultry Research and Extension, 7361 DA Beekbergen, Netherlands.

Denenberg, V. H. 1964. Critical periods, stimulus input, and emotional reactivity: A theory of infantile stimulation. *Psychol. Rev.* 71:335–51.

———. 1967. Stimulation in infancy, emotional reactivity, and exploratory behavior. In *Biology and behavior: Neurophysiology and emotion,* ed. D. C. Glass. New York: Russell Sage Foundation and Rockefeller University Press.

Dess, N. K., Linwick, D., Patterson, J., and Overmeier, J. B. 1983. Immediate and proactive effects of controllability and predictability on plasma cortisol responses to shock in dogs. *Behav. Neurosci.* 97:1005–16.

Dickinson, A. 1980. *Contemporary animal learning.* Cambridge: Cambridge University Press.

Draper, W. A., and Bernstein, I. S. 1963. Stereotyped behaviour and cage size. *Percept. Mot. Skills* 16:231–34.

Duncan, I. J. H., and Filshie, J. H. 1980. The use of radiotelemetry devices to measure temperature and heart rate in domestic fowl. In *A handbook on biotelemetry and radio tracking,* ed. C. J. Amlaner and D. W. Macdonald, 579–88. Oxford: Pergamon Press.

Eberhardt, J. A., Keverne, E. B., and Meller, R. E. 1980. Social influences on plasma testosterone levels in male talapoin monkeys. *Horm. Behav.* 14:247–65.

Einon, D. F., Humphreys, A. P., Chivers, S. M., Field, S., and Naylor, V. 1981. Isolation has permanent effects upon the behavior of the rat but not the mouse, gerbil, or guinea pig. *Dev. Psychobiol.* 14:343–55.

Einon, D. F., Morgan, M. J., and Kibbler, C. C. 1978. Brief periods of socialization and later behaviour in the rat. *Dev. Psychobiol.* 11:213–25.

Eisenberg, J. F., and Kleiman, D. G. 1977. The usefulness of behaviour studies in developing captive breeding programmes for mammals. *Int. Zoo Yrbk.* 17:81–88.

Engel, G. L. 1967. A psychological setting of somatic disease: The giving up-given up complex. *Proc. R. Soc. Med.* 60: 553–55.

Erwin, J., and Deni, R. 1979. Strangers in a strange land: Abnormal behaviors or abnormal environment? In *Captivity and behavior,* ed. J. Erwin, T. L. Maple, and G. Mitchell, 1–28. New York: Van Nostrand Reinhold.

Fentress, J. C. 1976. Dynamic boundaries of patterned behaviour: Interaction and self-organization. In *Growing points in ethology,* ed. P. P. G. Bateson and R. A. Hinde, 135–69. Cambridge: Cambridge University Press.

Frank, H., and Frank, M. G. 1982. On the effects of domestication on canine social development and behavior. *Appl. Anim. Behav. Sci.* 8:507–25.

Frankham, R., Hemmer, H., Ryder, O. A., Cothran, E. G., Soulé, M. E., Murray, N. D., and Snyder, M. 1986. Selection in captive populations. *Zoo Biol.* 5:127–38.

Fraser, D. 1975. The effect of straw on the behavior of sows in tether stalls. *Anim. Prod.* 21:59–68.

Fride, E., and Weinstock, M. 1984. The effects of prenatal exposure to predictable or unpredictable stress on early development in the rat. *Dev. Psychobiol.* 17 (6): 651–60.

Friend, T. H., Dellmeier, G. R., and Gbur, E. E. 1985. Comparison of four methods of calf confinement. I. Physiology. *J. Anim. Sci.* 60:1095–1103.

Garshelis, D. L., and Pelton, M. R. 1980. Activity of black bears in the Great Smoky Mountains National Park. *J. Mammal.* 61: 8–19.

Gendreau, P. E., Freedman, N., Wilde, G. J. S., and Scott, G. D. 1968. Stimulation seeking after seven days of perceptual deprivation. *Percept. Mot. Skills* 26:547–50.

Gentsch, C., Vichtsteiner, M., and Feer, H. 1981. Locomotor activity, defecation score, and corticosterone levels during an open-field exposure: A comparison among individually and group-housed rats, and genetically selected rat lines. *Physiol. Behav.* 27:183–86.

Glatston, A. R., Geilvoet-Soeteman, E., Hora-Pecek, E., and Hooff, J. A. R. A. M. van. 1984. The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, *Saguinus oedipus oedipus. Zoo Biol.* 3:241–53.

Glickman S. E., and Scroges, R. W. 1966. Curiosity in zoo animals. *Behaviour* 26:151–88.

Goldfoot, D. A. 1977. Rearing conditions which support or inhibit later sexual potential of laboratory monkeys: Hypothesis and diagnostic behavior. *Lab. Anim. Sci.* 27:548–56.

Gould, E., and Bres, M. 1986. Regurgitation and reingestion in captive gorillas: Description and intervention. *Zoo Biol.* 5: 241–50.

Greenough, W. T. 1976. Enduring brain effects of differential experience and training. In *Neural mechanisms of learning and memory,* ed. M. R. Rosenzweig and E. L. Bennett, 255–78. Cambridge, Mass.: MIT Press.

Hale, E. B. 1969. Domestication and the evolution of behavior. In *The behaviour of domestic animals,* 2d ed., ed. E. S. E. Hafez, 22–42. London: Bailliere, Tindall and Cassell.

Hancocks, D. 1980. Bringing nature into the zoo: Inexpensive solutions for zoo environments. *Int. J. Stud. Anim. Prob.* 1 (3): 170–77.

Hannah, A. C., and Brotman, B. 1990. Procedures for improving maternal behavior in captive chimpanzees. *Zoo Biol.* 9:233–40.

Harlow, H. F., and Harlow, M. K. 1965. The affectional systems. In *Behavior of non-human primates,* vol. 2, ed. A. M. Schrier, 287–334. Orlando, Fla.: Academic Press.

Harlow, H. F., Harlow, M. K., Dodsworth, R. O., and Arling, G. L. 1966. Maternal behavior of rhesus monkeys deprived of mothering and peer associations in infancy. *Proc. Am. Phil. Soc.* 110: 58–66.

Harlow, H. F., and Zimmerman, R. R. 1959. Affectional responses in the infant monkey. *Science* 130:421–32.

Harvey, P. W., and Chevins, P. F. D. 1985. Crowding pregnant mice affects attack and threat behavior of male offspring. *Horm. Behav.* 19:86–97.

Hebb, D. O. 1949. *The organization of behavior.* New York: Wiley.

Hediger, H. 1934. Uber Bewegungsstereotypien bei gehaltenen Tieren. *Revue Suisse de Zoologie* 41:349–56.

———. 1938. Ergebnisse tierpsychologischer Forschung im Zirkus. *Naturwissenschaft* 26:16.

———. 1964. *Wild animals in captivity.* New York: Dover Publications.

———. 1968. *The psychology and behaviour of animals in zoos and circuses.* New York: Dover Publications.

———. 1970. *Man and animal in the zoo.* New York: Delacorte Press.

Hennessy, M. B., Heyback, J. P., Vernikos, J., and Levine, S. 1979. Plasma corticosterone concentrations sensitively reflect levels of stimulus intensity in the rat. *Physiol. Behav.* 22:821–25.

Hennessy, J. W., and Levine, S. 1979. Stress, arousal, and the pituitary-adrenal system: A psychoendocrine hypothesis. In *Prog. Psychobiol. Physiol. Psychol.* 8:133–78.

Henry, J. P., and Stephens, P. M. 1977. *Stress, health, and the social environment: A sociobiologic approach to medicine.* New York: Springer Verlag.

Hess, E. H. 1973. *Imprinting.* New York: Van Nostrand Reinhold.

Hintz, H. F., Sedgewick, C. J., and Schryver, H. F. 1976. Some observations on digestion of a pelleted diet by ruminants and nonruminants. *Int. Zoo Yrbk.* 16:54–62.

Hofer, M. A. 1981. Parental contributions to the development of their offspring. In *Parental care in mammals,* ed. D. J. Gubernick and P. H. Klopfer, 77–105. New York: Plenum Press.

Holzapfel, M. 1938. Ber Bewegungsstereotypien bei gehaltenen Säugern. I. Mitt. Bewegungsstereotypien bei Caniden und Hyaena. II. Mitt. Das "Weben" der Pferde. *Z. Tierpsychol.* 2: 46–72.

———. 1939. Die Entstehung einiger Bewegungsstereotypien bei gehaltenen Säugern und Vogeln. *Revue Suisse de Zoologie* 46: 567–80.

Hooff, J. A. R. A. M. van. 1973. The Arnhem Zoo chimpanzee consortium: An attempt to create an ecologically and socially acceptable habitat. *Int. Zoo Yrbk.* 13:195–203.

Hughes, R. N. 1968. Behaviour of male and female rats with free choice of two environments differing in novelty. *Anim. Behav.* 16:92–96.

Hutchins, M., Hancocks, D. H., and Crockett, C. 1984. Naturalistic solutions to the behavioral problems of captive animals. *Der Zoologische Garten,* n.f. Jena, 54:28–42.

Immelmann, K. 1972. Sexual and other long-term aspects of imprinting in birds and other species. In *Advances in the study of behavior,* vol. 4, ed. D. S. Lehrman, R. A. Hinde, and E. Shaw. 147–174. New York: Academic Press.

Inglis, I. R. 1975. Enriched sensory experience in adulthood increases subsequent exploratory behavior in the rat. *Anim. Behav.* 23:932–40.

———. 1983. Towards a cognitive theory of exploratory behavior. In *Exploration in animals and man,* ed. J. Archer and L. Birke, 72–103. Berkshire, U.K.: Van Nostrand Reinhold.

Inhelder, E. 1955. Zur Psychologie einiger Verhaltensweisen-besonders des Spiels- von Zootieren. *Z. Tierpsychol.* 12: 88–144.

Jesberger, J. A., and Richardson, J. S. 1985. Animal models of depression: Parallels and correlates to severe depression in humans. *Biol. Psychiatry* 20:764–84.

Joffe, J. M., Rawson, R. A., and Mulick, J. A. 1973. Control of their environment reduces emotionality in rats. *Science* 180: 1383–84.

Kant, G. J., Anderson, S. M., and Mougey, E. H. 1987. Effects of chronic stress on plasma corticosterone, ACTH, and prolactin. *Physiol. Behav.* 40:775–79.

Kavanau, J. L. 1963. Compulsory regime and control of environment in animal behavior. I. Wheel-running. *Behaviour* 20: 251–81.

———. 1964. Behavior, confinement, adaptation, and compulsory regime in laboratory studies. *Science* 143:143.

Keeler, C. E. 1975. Genetics of behavior variations in color phases of the red fox. In *The wild canids: Their systematics, behavioral ecology, and evolution,* ed. M. W. Fox, 399–413. New York: Van Nostrand Reinhold.

Kelley, K. W. 1985. Immunological consequences of changing environmental stimuli. In *Animal stress,* ed. G. P. Moberg, 193–224. Bethesda, Md.: American Physiological Society.

Keulen-Kromhout, G. van. 1978. Zoo enclosures for bears: Their influence on captive behavior and reproduction. *Int. Zoo Yrbk.* 18:177–86.

Kish, G. B. 1966. Studies of sensory reinforcement. In *Operant behavior,* ed. W. K. Honig, 10–159. New York: Appleton-Century-Crofts.

Kleiman, D. 1980. The sociobiology of captive propagation. In *Conservation biology: An evolutionary-ecological perspective,* ed. M. E. Soulé and B. A. Wilcox, 243–62. Sunderland, Mass.: Sinauer Associates.

Koolhaas, J. M., Schuurman, T., and Fokkema, D. S. 1985. Social behaviour of rats as a model for the psychophysiology of hypertension. In *Biobehavioral bases of coronary heart disease,* ed. T. M. Dembrovski, T. H. Schmidt, and G. Blumchen, 391–400. Basel: Karger.

Levine, S. 1966. Infantile stimulation and adaptation to stress. In *Endocrines and the central nervous system,* ed. R. Levine, 280–91. Baltimore: Williams and Wilkins.

———. 1983. Coping: An overview. In *Biological and psychological basis of psychosomatic disease,* ed. H. Ursin and R. Murison, 15–26. Oxford: Pergamon Press.

———. 1985. A definition of stress? In *Animal stress,* ed. G. P. Moberg, 51–70. Bethesda, Md.: American Physiological Society; Baltimore, Md.: Williams and Wilkins.

———. 1986. Maternal deprivation, stress, and development. Paper presented at the NIH Conference on the Mechanisms of Physical and Emotional Stress, 6–8 November, Bethesda, Md.

Lewis, M., and Goldberg, S. 1969. Perceptual-cognitive development in infancy: A generalized expectancy model as a function of the mother-infant interaction. *Merril-Palmer Q. Behav. Dev.* 15:81–100.

Maple, T. L., and Finlay, T. W. 1987. Post-occupancy evaluation in the zoo. *Appl. Anim. Behav. Sci.* 18:5–18.

———. 1989. Applied primatology in the modern zoo. *Zoo Biol.* suppl. 1:101–16.

Markowitz, H. 1975. New methods for increasing activity in zoo animals: Some results and proposals for the future. In *Centennial Symposium on Science and Research,* 151–62. Topeka: Hill's Division, Riviana Foods.

Mason, G. J. 1991a. Stereotypies: A critical review. *Anim. Behav.* 41:1015–37.

———. 1991b. Stereotypies and suffering. *Behav. Processes* 25: 103–15.

Mason, J. W. 1971. A reevaluation of the concept of "nonspecificity" in stress theory. *J. Psychiatr. Res.* 8:323–33.

Mason, W. A. 1978. Social experience and primate cognitive development. In *The development of behavior,* ed. G. M. Burghardt and M. Bekoff, 233–53. New York: Garland STPM.

Mason, W. A., and Berkson, G. 1975. Effects of maternal mobility on the development of rocking and other behaviors in rhesus monkeys: A study with artificial mothers. *Dev. Psychobiol.* 8: 197–211.

Mason, W. A., Brady, J. V., and Tolliver, G. A. 1968. Plasma and urinary 17-hydroxycorticosteroid responses to 72-hr avoidance sessions in the monkey. *Psychosom. Med.* 30:608–30.

Mayr, E. 1958. Behavior and systematics. In *Behavior and evolution,* ed. A. Roe and G. G. Simpson, 341–62. New Haven: Yale University Press.

Meder, A. 1985. Integration of hand-reared gorilla infants in a group. Zoo *Biol.* 4:1–12.

Meyer-Holzapfel, M. 1968. Abnormal behavior in zoo animals. In *Abnormal behavior in animals,* ed. M. W. Fox, 476–503. Philadelphia: W. B. Saunders.

Miller, S. M. 1980. When is a little information a dangerous thing? Coping with stressful events by monitoring versus blunting. In *Coping and health,* ed. S. Levine and H. Ursin, 145–69. New York: Plenum Press.

Mineka, S., and Henderson, R. W. 1985. Controllability and predictability in acquired motivation. *Annu. Rev. Psychol.* 36: 495–529.

Mineka, S., and Suomi, S. 1978. Social separation in monkeys. *Psychol. Bull.* 85:1376–1400.

Mitchell, G. 1970. Abnormal behavior in primates. *Primate Behav.* 1:195–249.

Moberg, G. P. 1985a. Biological response to stress: Key to assessment of animal well-being? In *Animal stress,* ed. G. P. Moberg, 27–50. Bethesda, Md.: American Physiological Society.

———. 1985b. Influence of stress on reproduction: Measure of well-being. In *Animal stress,* ed. G. P. Moberg, 245–67. Bethesda, Md.: American Physiological Society.

Moltz, H. 1965. Contemporary instinct theory and the fixed action pattern. *Psychol. Rev.* 72:27–47.

Money, J., and Ehrhardt, A. A. 1972. *Man and woman, boy and girl.* Baltimore: Johns Hopkins University Press.

Montgomery, K. C. 1953. Exploratory behavior as a function of "similarity" of stimulus situations. *J. Comp. Physiol. Psychol.* 46:129–33.

Moore, C. L. 1984. Maternal contributions to the development of masculine sexual behavior in laboratory rats. *Dev. Psychobiol.* 17:347–56.

Moretto, D., Paclik, L., and Fleming, A. 1986. The effects of early rearing environments on maternal behavior in adult female rats. *Dev. Psychobiol.* 19:581–91.

Mormede, P., Dantzer, R., Bluthe, R. M., and Caritez, J. C. 1984. Differences in adaptive abilities of three breeds of Chinese pigs. *Génétique, Sélection, et Evolution* 16:85–102.

Morris, D. 1964. The response of animals to a restricted environment. *Symp. Zool. Soc. Lond.* 13:99–118.

———. 1966. Abnormal rituals in stress situations: The rigidification of behavior. *Phil. Trans. R. Soc. Lond.* 251:327–30.

Odberg, F. O. 1978. *Abnormal behaviours: (stereotypies).* Proceedings of the First World Congress of Ethology Applied to Zootechnics, Madrid, 475–80.

———. 1987. The influence of cage size and environmental enrichment on the development of stereotypies in bank voles *(Clethrionomys glareolus). Behav. Processes* 14:155–76.

O'Keefe, J., and Nadel, L. 1978. *The hippocampus as a cognitive map.* Oxford: Clarendon Press.

Osborne, S. E. 1977. The free food (contra–freeloading) phenomenon: A review and analysis. *Anim. Learn. Behav.* 5:221–35.

Overmeier, J., Patterson, J., and Weilkiewicz, R. M. 1980. Environmental contingencies as sources of stress in animals. In *Coping and health,* ed. S. Levine and H. Ursin, 1–37. New York: Plenum Press.

Overmeier, J., and Seligman, M. E. P. 1967. Effects of inescapable shock upon subsequent escape and avoidance responding. *J. Comp. Physiol. Psychol.* 63:28.

Paulk, H. H., Dienske, H., and Ribbens, L. G. 1977. Abnormal behavior in relation to cage size in rhesus monkeys. *J. Abnorm. Psychol.* 86:87–92.

Price, E. O. 1978. Genotype versus experience effects on aggression in wild and domestic Norway rats. *Behaviour* 64:340–53.

———. 1984. Behavioral aspects of animal domestication. *Q. Rev. Biol.* 59:1–32.

Putten, G. van. 1980. Objective observations on the behaviour of fattening pigs. *Anim. Regul. Stud.* 3:105–18.

Ralls, K., Brugger, K., and Ballou, J. 1979. Inbreeding and juvenile mortality in small populations of ungulates. *Science* 206: 1101–3.

Reichlin, S. 1987. Basic research of hypothalamic-pituitary-adrenal neuroendocrinology: An overview. The physiological function of the stress response. In *Hormones and depression,* ed. U. Halbreich, 21–30. New York: Raven Press.

Restrepo, C., and Armario, A. 1987. Chronic stress alters pituitary-adrenal function in prepubertal male rats. *Psychoneuroendocrinology* 12 (5): 393–98.

Rideout, B. A., Gause, G. E., Benirschke, K., and Lasley, B. L. 1985. Stress-induced adrenal changes and their relation to reproductive failure in captive nine-banded armadillos *(Dasypus novemcinctus).* Zoo *Biol.* 4:129–37.

Riittinen, M. L., Lindroos, F., Kimanen, A., Pieninkeroinen, E., Pieninkeroinen, I., Sippola, J., Veilahti, J., Bergstrom, M., and Johansson, G. 1986. Impoverished rearing conditions increase stress-induced irritability in mice. *Dev. Psychobiol.* 19: 105–11.

Roberts, M. 1982. Demographic trends in a captive population of red pandas *(Ailurus fulgens).* Zoo *Biol.* 1:119–26.

Rose, R. M. 1987. Endocrine abnormalities in depression and stress: An overview. In *Hormones and depression,* ed. U. Halbreich, 31–47. New York: Raven Press.

Rosenzweig, M. R., and Bennett, E. L. 1976. Enriched environments: Facts, factors and fantasies. In *Knowing, thinking, and believing,* ed. L. Petrinovich and J. L. McGaugh, 179–213. New York: Plenum Press.

Ruppenthal, G. C., Arling, G. L., Harlow, H. F., Sackett, G. P., and Suomi, S. J. 1976. A 10-year perspective of motherless mother monkey behavior. *J. Abnorm. Psychol.* 85:341–49.

Rushen, J. 1984. Stereotyped behaviour, adjunctive drinking, and the feeding period of tethered sows. *Anim. Behav.* 32:1059–67.

———. 1993. The "coping" hypothesis of stereotypic behaviour. *Anim. Behav.* 45:613–15.

Sackett, G. P. 1974. Sex differences in rhesus monkeys following varied rearing experiences. In *Sex differences in behavior,* ed. R. M. Richart and R. L. Vande Wiele, 99–122. New York: John Wiley and Sons.

Salzen, E. A. 1962. Imprinting and fear. *Symp. Zool. Soc. Lond.* 8:199–218.

———. 1970. Imprinting and environmental learning. In *Development and evolution of behavior,* ed. L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt. San Francisco: W. H. Freeman.

Scott, J. P. 1954. The effects of selection and domestication upon the behavior of the dog. *J. Natl. Cancer Inst.* 15:739–58.

Seligman, M. E. P., and Meyer, B. 1968. Chronic fear produced by unpredictable electric shock. *J. Comp. Physiol. Psychol.* 66: 402–11.

———. 1970. Chronic fear and ulcers in rats as a function of the unpredictability of safety. *J. Comp. Physiol. Psychol.* 73: 202–7.

Selye, H. 1936. A syndrome produced by diverse nocuous agents. *Nature* 138:32.

———. 1950. *Stress.* Montreal: Acta.

———. 1956. *The stress of life.* New York: McGraw Hill.

———. 1974. *Stress without distress.* London: Hodder and Stoughton.

Shoemaker, A. H. 1982. The effect of inbreeding and management on propagation of pedigree leopards. *Int. Zoo Yrbk.* 22: 198–206.

Singh, D. 1970. Preference for bar pressing to obtain reward over freeloading in rats and children. *J. Comp. Physiol. Psychol.* 73: 320–27.

Sluckin, W. 1968. Imprinting in guinea-pigs. *Nature* 220:1148.

Smith, A., Lindburg, D. G., and Vehrencamp, S. 1989. Effect of food preparation on feeding behavior of lion-tailed macaques. *Zoo Biol.* 8:67–75.

Sokolov, E. M. 1960. Neuronal models and the orienting reflex. In *The central nervous system and behavior,* ed. M. A. B. Brozier, New York: Josiah Macy Jr. Foundation.

Spinelli, J. S., and Markowitz, H. 1985. Prevention of cage-associated distress. *Lab Anim.* 14:19–28.

Stanton, M. E., Wallstrom, J., and Levine, S. 1987. Maternal contact inhibits pituitary-adrenal stress responses in preweanling rats. *Dev. Psychobiol.* 20:131–45.

Stein, D. G., Finger, S., and Hart, T. 1983. Brain damage and recovery: Problems and perspectives. *Behav. Neural Biol.* 37: 185–222.

Stevenson, M. F. 1983. The captive environment: Its effect on exploratory and related behavioural responses in wild animals. Chap. 7 in *Exploration in animals and man,* ed. J. Archer and L. Birke, 176–97. Berkshire, U.K.: Van Nostrand Reinhold.

Stolz, S. B., and Lott, D. F. 1964. Establishment in rats of a persistent response producing a net loss of reinforcement. *J. Comp. Physiol. Psychol.* 57:147.

Stoskopf, M. K. 1983. The physiological effects of psychological stress. *Zoo Biol.* 2:179–90.

Stott, D. H. 1973. Follow-up study from birth of the effects of prenatal stress. *Dev. Med. Child Neurol.* 15:770–87.

Suomi, S. J. 1986. Behavioral aspects of successful reproduction in primates. In *Primates: The road to self-sustaining populations,* ed. K. Benirschke, 331–40. New York: Springer Verlag.

Suomi, S. J., and Harlow, H. F. 1976. Social rehabilitation of separation-induced depressive disorders in monkeys. *Am. J. Psychiatry* 133:1279–85.

Thompson, W. R., Watson, J., and Charlsworth, W. R. 1962. The effects of prenatal maternal stress on offspring behavior in rats. *Psychol. Monogr.* 76 (557): 1–26.

Treus, V. D., and Lobanov, N. V. 1971. Acclimatization and domestication of the eland *Taurotragus oryx* at Askanya-Nova Zoo. *Int. Zoo Yrbk.* 11:147–56.

Uphouse, L. 1980. Reevaluation of mechanisms that mediate brain differences between enriched and impoverished' animals. *Psychol. Bull.* 88:215–32.

Ward, I. L. 1972. Prenatal stress feminizes and demasculinizes the behavior of males. *Science* 175:82–84.

Warren, J. M., Zerweck, C., and Anthony, A. 1982. Effects of environmental enrichment on old mice. *Dev. Psychobiol.* 15: 13–18.

Weinberg, J., and Levine, S. 1980. Psychobiology of coping in animals: The effects of predictability. In *Coping and health,* ed. S. Levine and H. Ursin, 39–60. New York: Plenum Press.

Weiner, I., Schnabel, I., Lubow, R. E., and Feldon, J. 1985. The effects of early handling on latent inhibition in male and female rats. *Dev. Psychobiol.* 18:291–97.

Weiss, J. M. 1968. Effects of coping responses on stress. *J. Comp. Physiol. Psychol.* 65:251–60.

Wiepkema, P. R. 1983a. On the significance of ethological criteria for the assessment of animal welfare. In *Indicators relevant to farm animal welfare,* ed. D. Schmidt, 69–79. Boston: M. Nijhoff.

———. 1983b. Umwelt and animal welfare. In *Farm animal housing and welfare,* ed. S. H. Baxter, M. R. Baxter, and J. A. C. MacCormack, 45–50. The Hague: Martinus Nijhoff.

Wilson, S. F. 1982. Environmental influences on the activity of captive apes. *Zoo Biol.* 1:201–9.

Winkelstraeter, K. H. 1960. Das Betteln der Zoo-Tiere (Diss.) Berlin: Hans Huber.

32

Communication and Social Behavior

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Communication and social behavior increasingly are being considered by zoo biologists as important factors in planning management programs for captive mammals (e.g., Erwin 1986; Maple and Finlay 1986; Suomi 1986; Snowdon 1989). Educators too are quick to cite the advantages of designing zoo exhibits that promote natural communication patterns and social interactions among animals (e.g., van Hooff 1986; Maple and Finlay 1989). Our objective here is to review briefly the current theory of social communication and to illustrate the advantages of applying this knowledge to the management of captive mammals. This chapter is organized into four major sections: (1) an introductory review of communication theory, (2) a discussion of the effects of environmental design on communication, (3) a proposal for improving animal management practices by studying communication and social behavior, and (4) a brief discussion of the advantages of studying communication and social behavior in a zoo setting.

Social behavior can be defined as any action directed by an individual toward another member of its own species (Wilson 1975). The result of such an action is to influence the social relationships between conspecifics (Fentress, Fiels, and Parr 1978; Poole 1985). Social behaviors include both competitive behaviors, such as aggressive displays and fighting, and cooperative behaviors, such as predator detection, food sharing, and parental care. A necessary assumption in the study of social behavior is that individuals *do* actively affect the behavior of their conspecifics. This assumption is also the essence of animal communication theory. In fact, operationally, we can say that communication occurs when one individual's actions provide a signal that changes the behavior of another individual (Wiley 1983). Thus, communication is central to all considerations of social behavior.

MAMMALIAN COMMUNICATION: AN INTRODUCTORY REVIEW

Animal communication has been the subject of numerous reviews (Smith 1977; Green and Marler 1979; Halliday and Slater 1983; and others). The details of mammalian communication are scattered widely in the scientific literature, but introductions to the subject are provided by Ewer (1968), Sebeok (1968, 1977), Eisenberg (1981), Walther (1984), and Poole (1985).

Animal communication will be defined here as "the process in which actors use specially designed signals or displays to modify the behavior of reactors" (Krebs and Davies 1993, 349). It is assumed that the sender-receiver relationship is in some way the result of natural selection so that the sender benefits, on average, from both the signal transmission and the response of the receiver. This requirement excludes cases of information transfer that have no selective advantage. For example, a mouse rustling in the grass might transfer information to a nearby owl, but we do not consider this communication.

An animal's communication signals represent wasted energy if no other individual receives and responds to them (Smith 1977). Communication, therefore, becomes functional only when there is a response, although the response to a specific signal may or may not be immediately evident to a human observer. Also, the response to a signal is not always an overt behavioral one; many communication messages cause salient hormonal changes (e.g., responses to mouse pheromones, reviewed by Bronson and Macmillan 1983). Likewise, the response might not occur until there has been an additive effect resulting from repeated signaling (Schleidt 1973). The animal's response—immediate or delayed, behavioral or physiological—must be detected by an investigator to demonstrate that communication has occurred.

Component Analysis of Mammalian Communication

Mammalian communication has been analyzed systematically from several different theoretical perspectives. One method of analysis is to reduce the system to its four component parts: (1) the sender, (2) the communication channel and signal, (3) the receiver, and (4) noise. The communication process originates with the sender. When studying signal evolution, it is the benefit gained by the sender that is of primary importance. Benefits may be direct, as when an animal's signal attracts a potential mate, or they may be more indirect, as when an animal sounds an alarm call to warn its conspecifics. Some authors suggest that an alarm caller may promote the survival of its own genes by helping related animals who carry some of the same genes as the caller (for a discussion of such "inclusive fitness," see Wilson 1975).

Communication Channels and Signals

Collectively, the 4,100 extant mammal species possess a large and diverse repertoire of information transfer methods. Mammalian signals may be transmitted through any one of four sensory channels: optical, acoustic, chemical, or tactile. Each channel has a unique set of physical attributes that affects its use as a means of transferring information between animals. Discussions are available for optical signals (Hailman 1977), chemical signals (Eisenberg and Kleiman 1972; Albone 1984; Brown and Macdonald 1987), auditory signals (Busnel 1977; Morton 1982; Tembrock 1989), and tactile signals (Eisenberg and Golani 1977; Geldard 1977).

Optical Signals. Species possessing well-developed optical signals generally are diurnal; thus the best examples within the Mammalia are found in primates (reviewed by Oppenheimer 1977; Gautier and Gautier 1977) and in ungulates (reviewed by Walther 1984) (fig. 32.1). Visual signals do not travel around corners or through structurally complex environments, and the distance over which they can be transmitted is limited by the size of the signaler (Slater 1985). These physical limitations, together with the fact that most mammals are small and nocturnal, account for the rather limited use of long-distance visual signaling by mammals.

Virtually all species, however, practice close-range optical signaling through visual displays such as piloerection. Piloerection, an increase in the apparent body size by erection of the hair, is a widely observed optical signal. Prominently displayed genitalia are also often used as visual signals. In the pig-tailed langur, *Nasalis (=Simias) concolor* (Tenaza 1989), some other Old World monkeys (Dixson 1983), and the chimpanzee, *Pan troglodytes* (Goodall 1986), the female's anogenital area swells and becomes brightly colored during the periovulatory period. Another frequently cited example of genitalia signaling is found in the vervet monkey, *Chlorocebus (=Cercopithecus) aethiops:* adult males have a bright orange prepuce and blue scrotum, which are displayed by dominant individuals.

Evolutionary ritualization has resulted in some visual signals that appear exaggerated; such signals are associated with bright colors and are displayed through stereotypic behavioral patterns (Halliday and Slater 1983). The "open-mouthed gape," with exposure of the pink mucous membranes and teeth, is an example of a ritualized threat display that is employed by many mammals. It is noteworthy, however, that interspecific variation in signal meaning does occur. In many *Macaca* species, for example, facial expressions with baring of the teeth are exclusively shown by the *lower*-ranking of two partners; that is, they are submissive signals, not aggressive ones (de Waal 1987).

Acoustic Signals. Auditory signals travel out in all directions and bend around corners; therefore, sound is not

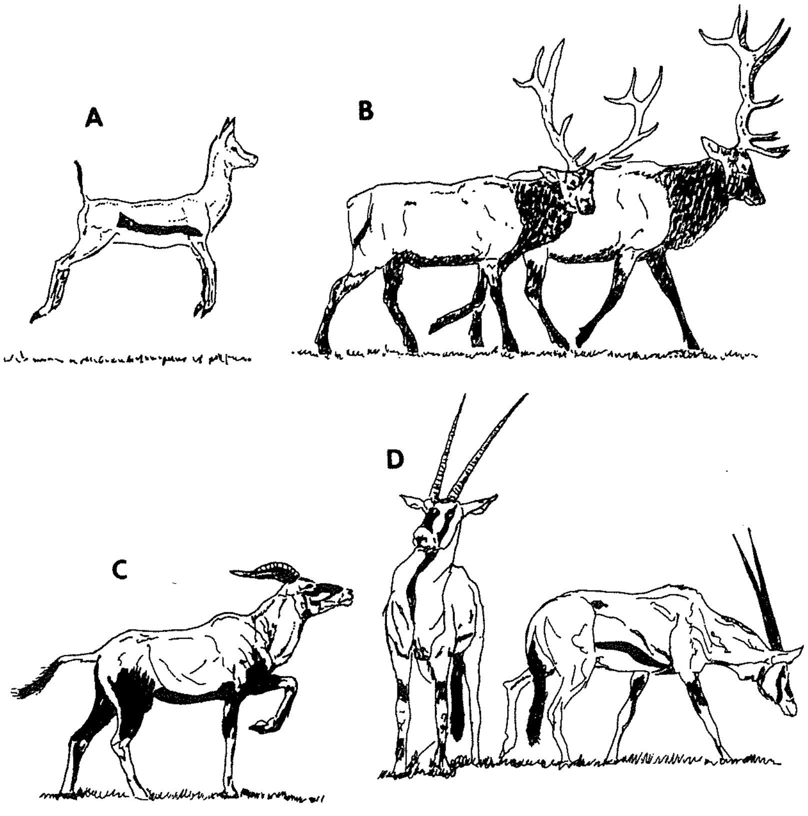

FIG. 32.1. Mammalian visual signals have many different meanings, but four especially important categories for zoo biologists to recognize are displays of alarm, aggression, courtship, and social status. *(A)* "Stotting" alarm in Thomson's gazelle, *Gazella thomsonii.* *(B)* "Parallel march" in an aggressive encounter of bull elk, *Cervus canadensis.* *(C)* "Head-up-angled-foreleg display" of a courting bull topi, *Damaliscus korrigum.* *(D)* "Broadside display" of a dominant bull oryx, *Oryx gazella,* to a withdrawing subordinate. (Drawings adapted from Walther 1984.)

generally a private channel of communication (see Busnel 1963, 1977). It is, however, a good means of advertising, provided that the animal is large enough to generate sufficient volume (Slater 1985). Sound communication also has the advantage that a great deal of information can be transmitted rapidly. The frequency, volume, and tonal qualities of sound can be modulated quickly, to a much greater extent than is possible with visual, chemical, or tactile signals. Vocal sound can be easily and rapidly modified by changes in the shape of the buccal cavity, and in some species (e.g., the siamang, *Hylobates syndactylus*), by special elastic vocal sacs.

Sounds produced by mammals include both vocalizations and nonvocal signals. Vocalizations, produced by vibration of the vocal cords, range in frequency from about 2 kHz in some large mammals to the ultrasound (greater than 20 kHz and as high as 100 kHz) of some bats, insectivores, and rodents (for a review of ultrasound, see Sales and Pye 1974). In general, the smaller the animal, the smaller its vocal cords, and hence the higher the frequency of its sounds.

Some gazelles and deer produce sound in their noses by vibrating cartilaginous structures, and cetaceans use their blowhole passages to create signals. In other nonvocal auditory signals, many rodents and ungulates grind their teeth (Eisenberg 1981; Walther 1984); gorillas, *Gorilla gorilla,* beat their chests (Fossey 1983); chimpanzees hit the ground with hands and sticks (Goodall 1986); rufous elephant shrews, *Elephantulus rufescens,* kangaroo rats, *Dipodomys,* and skunks, *Mephitis mephitis,* stamp the ground with their hind feet (foot-drumming is reviewed by Roeper 1981); and tenrecs, *Centetes* and *Hemicentetes,* produce sounds by rattling their quills (Eisenberg and Gould 1970). It is known that elephants, *Elephas maximus* and *Loxodonta africana,* communicate with infrasounds (frequencies less than 20 Hz, the lower limit of human hearing); the exact sound production mechanism is unclear (Payne, Langbauer, and Thomas 1986).

Chemical Signals. In recent years, it has become evident that many mammalian odors function as chemical signals that have important effects on reproduction and social behavior (Eisenberg and Kleiman 1972; Johnston 1983; Albone 1984; Brown and Macdonald 1987). Mammals are particularly rich in sources of chemical signals, which include accessory glands of the reproductive tract, feces, salivary glands, skin glands, and urine (reviewed by Adams 1980; Albone 1984). Chemical signals can either be released into the air or be dispersed by scent marking, specialized behavior patterns that function to deposit odorous substances on the ground or on environmental objects (Johnson 1973). In general, small and nocturnal species have the best-developed scent glands (reviewed by Quay 1977; Adams 1980; Sokolov 1982).

The advantages of communicating with chemical signals include their ability to be used effectively at night; the ability of air-dispersed compounds to diffuse around obstacles; energetically cheap components; minimal energy transmission requirements; a high potential range; a large information content; and persistence in time, which permits delayed communication (Wilson and Bossert 1963; Wilson 1968, 1975; Sebeok 1968, 1972). However, the relatively slow fade-out time of chemical signals can be a disadvantage because it results in rather static messages that cannot be altered abruptly (Wilson 1975). For example, the use of chemical signals usually would be disadvantageous, compared with auditory or visual signals, when conveying information about a sender's rapidly changing motivational state. Another disadvantage of the use of chemical signals is their slow transmission speed, which results in the inability to transmit messages quickly over long distances.

In the last thirty years, considerable progress has been made in describing the chemical communication systems of a variety of mammals, yet few general principles of mammalian olfactory communication have emerged. Debate also continues about the adaptive function of scent marking (Ralls 1971; Gosling 1982).

Tactile Signals. Communication by touch has been poorly studied, and its importance probably has been underestimated (Geldard 1977). Although the amount of information transferred by tactile signals is small compared with other communication modalities, it is certain that many nocturnal, highly social, and burrowing animals rely heavily on this type of signaling (Poole 1985). Allogrooming, in addition to its cleaning function (Hutchins and Barash 1976), is an important form of communication. "Snap biting" is a common warning signal practiced by rodents, carnivores, and primates. Body rubbing occurs in a sexual or affectional context in such species as tenrecs, *Hemicentetes* (Poduschka 1977), and domestic cats, *Felis catus* (Leyhausen 1979). Other examples of behaviors in which tactile information may be exchanged by mammals include nuzzling, licking, and kissing (e.g., prairie dogs, *Cynomys ludovicianus:* King 1959), huddling, and playing.

The Receiver

To a human observer, an animal's perception of a signal appears as a unitary process. However, it is wise to remember that for the vast majority of mammals, no single sensory modality is divorced from the others. The process of perception is influenced by a complex of internal and external factors that are often unknown to the observer. Each receiver enters a communication encounter with its own unique internal environment, which includes both its hormonal state and its set of previously learned experiences. These factors taken together influence an animal's specific response to any given signal.

Much has been written concerning the sensory abilities of vertebrates; recent reviews are available on vision (Levine 1985), hearing (Fay and Popper 1985), olfaction (Dodd and Squirrell 1980; Shirley 1984), and touch (Bullock, Orkand, and Grinnel 1977).

Noise

Any disturbance that alters the information content of a signal is called noise. Most communication takes place within a noisy channel. Hailman (1977) distinguished two kinds of noise: that which physically changes the signal during transmission (transmission noise) and that which overwhelms the signal with extraneous entropy (detection noise). We can expect animals to maximize efficiency by operating their communication systems as close to the ambient noise level as possible (Schleidt 1973).

Noise generated by environmental factors (e.g., wind, humidity, and temperature) has been examined for its effects on acoustic signals (Piercy and Embelton 1977; Wiley and Richards 1978), chemical signals (Wilson 1968; Regnier and Goodwin 1977), and optical signals (Hailman 1977). Noise in the acoustic channel results from both biological sources (e.g., choruses of amphibians, birds, and insects) and nonbiological sources (e.g., falling water, wind, and wind-blown vegetation). In the visual channel, background noise consists mainly of light reflections from vegetation, water, and the ground. Chemical communication is altered by the age of the scent mark, humidity, temperature, and the presence of the scent marks of other animals (Johnston and Schmidt 1979; Wellington, Beauchamp, and Wojciechowski-Metzler 1983).

ANIMAL COMMUNICATION AND THE ZOO ENVIRONMENT

The zoo environment should allow animals to express the full extent of their behavioral repertoire, or at least as much of it as is possible in captivity. The expression of natural behavior by zoo animals not only increases the welfare of the animals but also benefits education and research efforts. With regard to social behavior and communication, the issues include the provision of places to mark or display, the availability of natural spacing, visual contact between animals in different enclosures, and the reduction of noise.

Meeting the Display Needs of Captive Mammals

The display needs of mammals vary widely. Senders often position themselves, or their signals, so as to maximize the chances that their messages will be detected by conspecifics. Ewer (1973) notes that many carnivores go to considerable trouble (e.g., "hand standing" against a vertical tree) to place their anal gland scent well off the ground at the height of the receiver's nose. The rufous elephant shrew often deposits scent at conspicuous locations, for example, near well-delineated trail junctions (Koontz 1984). Some forest primates (e.g., blue monkeys, *Cercopithecus mitis*) call from characteristic heights, which apparently maximizes transmission distances by taking advantage of natural sound channels through the forest canopy (Brown 1989).

The relationship between animal communication and spatial use of enclosures remains largely unstudied for zoo mammals. A better understanding of this association would allow zoo architects to include "communication sites" in their exhibit designs, thereby enriching the environment for animal and visitor alike. In one study on enclosure use during scent marking, red pandas, *Ailurus fulgens*, were found to have significant preferences for particular marking sites, those being prominent points in the enclosure (Conover and Gittleman 1989). The objects they marked were upraised and near main travel routes. These results suggest that objects that the animals prefer to mark should be placed near food, water, latrines, and denning areas.

Natural Spacing

The availability of natural spacing is also important. Western tarsier females, *Tarsius bancanus*, are relatively solitary in captivity (Roberts and Kohn 1993). They sleep one to a nest box unless young offspring are present. (Adult males and females may be housed in pairs, but do not share nest boxes.) Females enforce these sleeping arrangements and keep the individual spacing maximized. The apparent reason for the females' behavior is that some male tarsiers are infanticidal. Whenever aggression over enclosure features (i.e., perching, resting, or eating sites) is a potential danger, several of these sites should be provided to minimize competition for them (Roberts and Kohn 1993). Enclosure size is important not only for individual spacing but also for the provision of sufficient flight distance for the animals. If sufficient flight distance is not provided so that animals may escape an aggressor or withdraw if disturbed, stereotypic behaviors such as pacing may arise (fennec fox, *Vulpes (=Fennecus) zerda,* Carlstead 1991).

Visual Contact between Animals in Different Enclosures

Visual contact between conspecific individuals or groups in separate enclosures can be beneficial, acceptable, or a source of stress. Allowing visual contact may provide beneficial social contact for individuals of a gregarious species that must be housed alone for some management reason, for example, animals recovering from injury or recently expelled from their group. In some species, visual contact between enclosures may add some stimulation. Hearn et al. (1978) reported that alternating the groups of common marmosets, *Callithrix jacchus,* housed in a centrally located exercise enclosure increased positive activity levels in the group in the central enclosure. While the change of enclosure itself aroused the central group, seeing all the other groups in the room also increased activity. This arrangement also provided excitement for the groups still in their home cages since they were able to interact with a new central group each time.

In other species, visual contact between groups or individuals has a definite negative effect. In territorial species, individuals may spend so much of their energy trying to "defend" their territories through visual and auditory displays and scent marking that they do not engage in other activities, such as eating or breeding or rearing offspring. This sort of interaction can also be a source of significant stress, causing health problems and/or a suppression of reproduction. In the Wisconsin Callitrichid Research Laboratory multiple conspecific groups of cotton-top tamarins, *Saguinus oedipus,* and pygmy marmosets, *Callithrix (=Cebuella) pygmaea,* were once housed in the same room, with most groups in visual contact. Breeding rates were low, and rates of successful rearing of offspring were even lower. When the groups were visually isolated from one another, simply by placing opaque sheets between the cages, levels of territorial displays significantly decreased and the rate of successful reproduction increased (C. T. Snowdon, pers. comm.).

Reducing Noise

The zoo environment should not only allow for the expression of natural behavior, it should also minimize disturbances (i.e., noise) that interfere with it. There are many sources of noise in the zoo, ranging from the obvious, such as other animals and zoo visitors, to the subtle, such as cleaning solutions and enclosure materials (see above for discussion of types of noise).

Maintenance Procedures as a Source of Noise. Analyses of all types of zoo noise, and their potential effects on animal communication and social behavior, are needed. Without question, the zoo is an acoustically noisy environment. But does this change the normal rate of vocalizations? Does "noise pollution" affect behavior or reproduction? Carlstead (1991) found that vacuum cleaner noise and unexpected loud noises in the keeper area were significantly correlated with stereotypic behavior in fennec foxes. She found that manual sweeping of the enclosure, instead of vacuuming, decreased stereotypic behavior.

Humans are notably poor in their olfactory abilities, and as a result, zoo biologists have largely ignored the biological significance of the captive animal's olfactory arena and olfactory "noise." For animals that scent mark, cleaning procedures can be very disruptive; cleaning too often and using scented materials can interfere with the transmission and effects of olfactory communication signals. For common marmosets and other callitrichids, for example, daily cleaning procedures may be very disruptive. In these species, scent marking by the dominant female is part of the mechanism that suppresses the reproduction of subordinate females and thus helps maintain group stability (Epple 1972). This suggests that keepers should allow the maximum time between cleanings that still permits cage hygiene to be maintained at an acceptable level. Another possibility is to refrain from cleaning some piece of enclosure "furniture" so that scent marks on it remain undisturbed.

The enclosure itself can be a source of noise and can impede beneficial communication. The vocalizations of large animals can travel through and around walls, but those of smaller animals, especially ultrasonic vocalizations, can be impeded by the thinnest wall. Fine mesh can be substituted for solid walls, thus allowing vocal communication between neighbors.

Other sources of "noise" can be found in the enclosure itself: ceramic tiles, which are easily cleaned but are reflective of sounds and cause echoes; and glass and metal, which reflect light, a type of visual noise. Many animals are sensitive to such reflections, especially of their own images. The images may be perceived as a threat, and the animals may spend a large amount of time threatening themselves in a mirror. Animals may also injure themselves trying to get at what they perceive as an intruder encroaching on their territory. Although such agonistic behaviors are likely to decrease over time, such environments can cause animals to engage in inappropriately high levels of aggression until they have become habituated.

Zoo Visitors as a Source of Noise. Visitors can affect the social behavior and communication of zoo animals by disrupting their typical interactions. Greater numbers of visitors may increase the rate of stereotypic behavior in fennec foxes (Carlstead 1991). Zoo visitors attempting to interact with animals may also have a stimulating effect and increase animal activity levels (Hosey 1989), an effect that may be positive or negative. This type of interaction should be discouraged if it disrupts the "natural" behavior of the animals or increases rates of stereotypic behavior. Glatston et al. (1984) found differences in the behavior of cotton-top tamarins that were on and off exhibit: the display group exhibited a lower overall rate of behavior. More importantly, the juvenile male in the display group received significantly more aggression than did the juvenile in the off-exhibit group. In all of the above cases, the larger the number of visitors, the greater the effect (Carlstead 1991; Glatston et al. 1984).

MONITORING SOCIAL DYNAMICS

Animal communication serves as an important regulator of social behavior. Signal evolution has allowed animals to influence more efficiently the actions of their conspecifics. Three typical circumstances in which communication affects social dynamics in the zoo environment are: (1) agonistic interactions, (2) affiliative interactions, and (3) maintenance of long-term social stability.

By quantifying social relationships, animal managers can establish normal behavioral baselines for exhibit groups. It is against these normal baselines that keepers can monitor their animals. By way of analogy, consider how a physician uses normal physiological values when diagnosing medical problems. Similarly, modern animal husbandry, especially for a species that cannot be routinely examined in hand because of its large size or delicate nature, requires behavioral baseline values. By periodically sampling the dynamics of an enclosure group, managers can detect significant changes in social relationships, thus allowing management intervention and the prevention of more serious problems (fig. 32.2).

Agonistic Interactions

Agonistic behavior (first defined by Scott and Fredericson 1951) refers to any activity related to fighting—aggressive, submissive, or defensive. The management of agonistic interactions among zoo animals is a critical component of all animal care programs. Situations that typically elicit aggressive behavior include antipredatory maneuvers, dominance interactions, parental disciplinary actions, sexual encounters, territorial disputes, and weaning conflicts (Wilson 1975). The most frequent situation in which aggressive behavior is shown by mammals is when they are defending assets that can be monopolized (Poole 1985). Typical assets defended are food supplies, living space, mates, offspring, resting sites, and the status that allows animals to acquire resources.

Despite the many potential resources to contest and the ample supply of anatomical weapons, life-threatening fights between mammals are infrequent in nature. This is largely due to the evolution of communication signals that function to mediate agonistic interactions between individuals. Threat, submissive, and defensive displays are used widely among the Mammalia. Ethologists define "displays" as ritualized behavioral acts that make information available to others (Smith 1977); their ritualization enhances communication by reducing message errors. Animal keepers can take advantage of these displays to obtain insight into the social dynamics of a group. It is important to note that in the wild, animals are free to escape each other, either temporarily or permanently (through dispersal); encounters that would

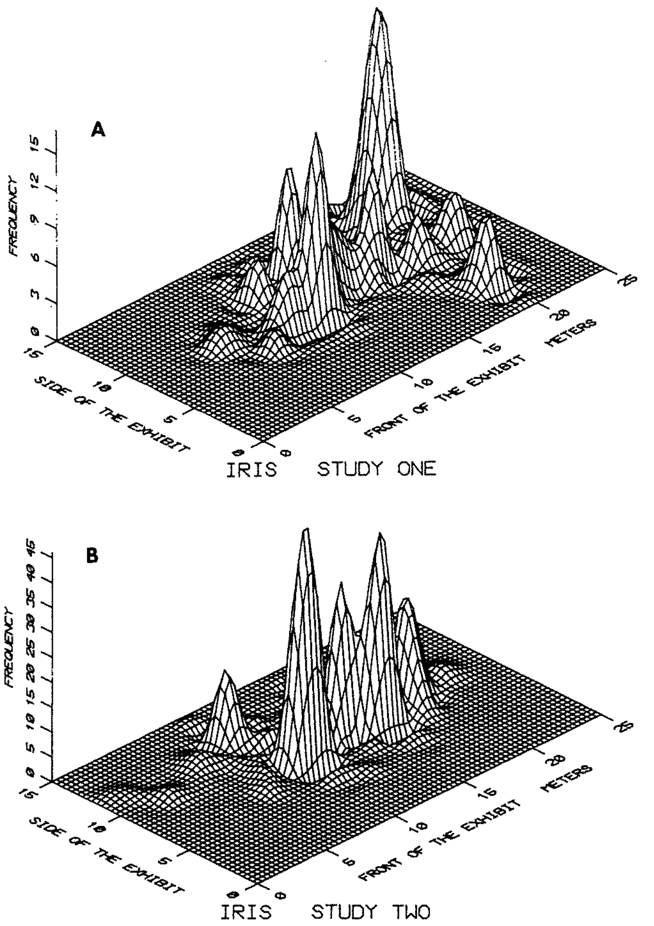

FIG. 32.2. Spatial analyses of exhibit use is one method of gaining insights into the social dynamics of zoo mammals. At the Wildlife Conservation Park, we conducted a spatial analysis of "Iris," a 3-year-old subordinate proboscis monkey, *Nasalis larvatus*, who was kept at first with her father and his harem; her father was later replaced by an unrelated male. *(A)* In "Study One," Iris spent a large part of her time in the right rear corner of the exhibit; she was being moderately ostracized by her father. *(B)* In "Study Two," Iris spent the majority of her time in the center of the exhibit, and was well integrated within the new male's troop.

easily resolve themselves in the wild may escalate in captivity, where animals cannot disperse.

Play-fighting and play-chasing have their own set of distinct communication signals and social conventions. Certain facial expressions and postures are reserved for play situations (Fagen 1981). These signals seem to say, "what follows is play and is not serious." A familiar case is the "play face" seen in some primates, such as the chimpanzee (Goodall 1986). It is important for animal keepers to be able to recognize the differences between play and true aggression. Thompson (chapter 34, this volume) provides a more extensive discussion of play.

A recurring problem faced by animal managers is the need to introduce new animals to socially established groups, or to reintroduce individuals to their own social group after a period of separation. By closely watching the levels and types of intragroup aggression, it is possible to ascertain how successful such an introduction will be. This "technique" can be particularly useful when new pairs or groups are formed. Newly introduced animals may be targets of aggression from other group members, as was the case in a group of sable antelope, *Hippotragus niger*, observed by Thompson (1993). She found that, because the types and levels of "typical" aggression within the group were known, it was possible to determine that the levels and types of aggression directed at a new individual were distinctly different. Butting was the typical form of aggression within the group, but with the introduction of a new female, displacements and chases increased. They were nine times more common toward the new female than toward other group members. These differences in the aggression directed toward the new female indicated that she was not perceived as part of the group.

There are methods of animal introduction that can be used to reduce aggression. These include (1) placing a screen door between individuals housed in adjacent enclosures until they are thoroughly familiar with each other (e.g., Roberts et al. 1987); (2) using "creep doors" through which one animal, usually a smaller juvenile, can retreat into an adjacent area but the other animals cannot (e.g., Inglett et al. 1989); and (3) transferring an individual's odors, usually in the form of feces or soiled bedding material, before the introduction of the new animal. While these and similar methods are employed by zoo biologists, there have been no studies comparing these techniques for different species. For example, it appears that transferring individual odors before an introduction in some species reduces aggression (e.g., rufous elephant shrews), but in other cases only makes matters worse (e.g., meerkats, *Suricata suricatta*). Introduction techniques for primates and nonprimate mammals are discussed by Watts and Meder (chap. 6) and Kranz (chap. 7, this volume) respectively.

Increases in or changes in the types of intragroup aggression can also be indicative of an upheaval about to occur in a group or pair. In some species, levels of low-intensity aggression (i.e., visual threats, etc.) may increase before an outbreak of high-intensity aggression occurs, as when an older offspring is being "expelled" from a group (e.g., golden lion tamarins, *Leontopithecus rosalia:* Inglett et al. 1989). This aggression may result in severe injury or death of an animal. By being aware of baseline behaviors, it is possible to foresee these violent expulsions and remove the appropriate group member in advance.

Submissive behaviors are also good clues to social instability. Submissive displays communicate that an individual will not retaliate, even if attacked. In golden lion tamarins and other callitrichids, subordinate individuals may grimace and produce a distinctive screeching vocalization. The subordinate animal may separate itself from a family group, watch other group members, and avoid the approach of some group members but not others. There may also be bursts of one or two individuals running about the cage horizontally in a loosely circular pattern (Inglett et al. 1989). Other commonly employed submissive displays include rolling over onto the back, exposing the abdomen, as in canids, felids, and rodents; and crouching, appearing as small as possible, as in ungulates and primates. Submissive displays typically are shown by young animals toward older ones, by females toward males, and by low-ranking individuals toward higher-ranking group members.

An animal that constantly performs submissive displays even when not being threatened or challenged may be in serious danger. In at least one case in the Wisconsin Callitrichid Laboratory, a juvenile cotton-top tamarin behaved very submissively when not being threatened and was violently expelled from his family group.

A change in sleeping arrangements may also indicate impending social upheaval or a lack of group (pair) cohesion. Cotton-top tamarins sleep together in a tight bundle; if one animal sleeps by itself, it is more than likely in the process of being expelled from the group. Alternatively, if animals that are newly introduced begin to sleep together, it is often a good indication that bonding has occurred.

Certain events in the life of a group or pair are potential trouble spots, such as births, weanings, and the presence of estrous females. In the Mayotte lemur, *Eulemur (=Lemur) fulvus mayottensis,* aggression levels are higher in captivity than those reported in the wild (Hosey 1989), especially during the birthing season, apparently due to aggression by males directed at infants and the defense of infants by females. Aggression levels also rise in Western tarsiers during late pregnancy and after the birth of infants (Roberts and Kohn 1993). Males of this species are also known to be infanticidal, and females enforce increased individual distances through displacements and chases.

Males of many species compete for females that are ovulating. Male red deer, *Cervus elaphus,* have disputes over females during the rut. They first engage in roaring matches, which escalate to "parallel walks." Then, if neither contestant has retreated, they resort to lowering antlers and charging (Clutton-Brock 1979). An animal's own signals may communicate the onset of estrus; for example, some female mammals signal receptivity by exhibiting proceptive behavior, in which they demonstrate their reproductive state by actively soliciting one or more males. Female shrews, *Blarina, Sorex,* and *Crocidura,* rufous elephant shrews, and golden hamsters, *Mesocricetus auratus,* which normally are dominant over males, become less aggressive toward any potential mate during estrus. In other species, such as chimpanzees and orangutans, *Pongo pygmaeus,* females display the genitalia. Some Old World monkeys and apes have conspicuous swollen circumgenital areas during estrus and also release chemical and behavioral signals (reviewed by Dixson 1983).

Monitoring Animal Health

Not only is it possible to determine how well animals are getting along with other animals in their group or enclosure through social behavior observations, it is also possible to monitor the health of individuals. By knowing the normal range of behaviors, one can detect changes when they occur and use them as indicators of animal health. Certain vocalizations are usually given only in times of distress (e.g., the distress call of pygmy marmosets, Pola and Snowdon 1975). Animals may huddle more with other group members if they are physically (physiologically) stressed. In those species in which infants are carried, the young may begin to ride again, or more frequently, if ill.

Communication between Animals and Zoo Keepers

An understanding of the animal's communication system can benefit the captive animal manager. Most importantly, it can enable one to know when one is in danger. An obvious and familiar example of an animal signal giving notice of potential danger is the rattle of a rattlesnake's tail. A common sign of potential danger among mammals is piloerection, a conservative signal of arousal in all mammals. As described above, animals will defend assets they perceive as threatened; they will defend them not only from each other, but from keepers as well. Keepers should be aware that the value of any given asset, and hence the defender's behavior in protecting it, can change quickly and dramatically. For example, a bull elephant is more likely to attack his keeper when the bull is tending an estrous cow rather than a nonestrous female. The danger is that a change in the value of an asset, in this case the female elephant, may not always be noticed readily by a human observer.

In the daily lives of most mammals, optical signals are of less importance than either acoustic or chemical signals, but for the zoo biologist, optical signals are the most important means of intercepting animal messages. This is a result of our primate heritage, and consequently, our largely visual perceptual world. By accurate translation of visual signals, animal keepers can work more sagely and better care for their charges.

Animal caretakers should be aware that many visual (and acoustic) displays are graded in intensity. These variations are correlated with the signal's precise meaning and the probability of the animal's subsequent behavior (e.g., its likelihood of attacking). Careless misreading of these signs by animal keepers has resulted in needless injuries. In general, the greater the magnitude of the message to be communicated, the more prolonged and intense the signal (Lorenz 1966). For example, the aggressive display of the rhesus macaque, *Macaca mulatta,* begins simply as a hard stare, escalates gradually as the monkey rises to a standing position, and then is most intense when the mouth opens and the head bobs up and down (Wilson 1972). If the opponent, perhaps an animal keeper, has not retreated at this point, the monkey may next attack.

It is also possible to use the animals' own signals to appease or to avoid dangerous encounters with them. Direct eye contact or staring is often perceived by animals as a threat. Therefore, by simply averting one's gaze, it is possible to appear nonthreatening. Making an animal aware of one's approach and presence is also a good tactic for avoiding an agonistic interaction. Researchers and trackers in the field use the "belch vocalization" of the mountain gorilla when approaching a group or when changing position within it (M. Robbins, pers. comm.). By imitating this vocalization the researchers can communicate their presence and movement near the group (Fossey 1983).

The fact that some mammals accept trainers as part of their dominance hierarchies allows keepers to control some large and potentially dangerous animals, such as elephants. Elephant trainers exploit the fact that elephants establish social hierarchies by assuming the position of the most dominant member of the herd (fig. 32.3). We do not know, however, whether this method has any deleterious side

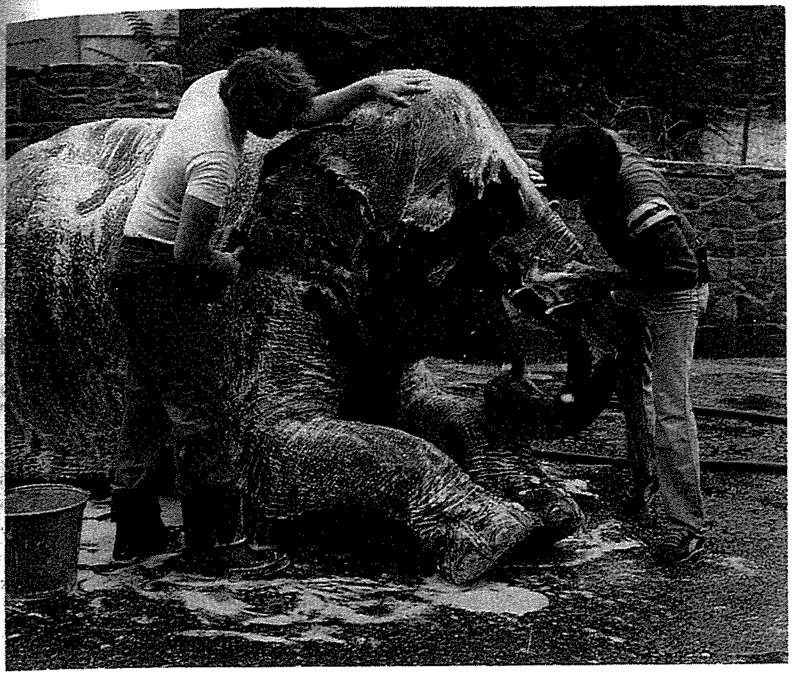

FIG. 32.3. Animal handlers are able to control some large mammals that follow social hierarchies by assuming the role of the dominant herd member.

effects. Some keepers have suggested that bull elephants dominated by human handlers might have lower testosterone levels, and hence suppressed reproductive potential, relative to bulls that are controlled by indirect means (e.g., via remotely operated hydraulic doors). Additionally, if the keeper who has assumed the dominant role is absent or has left the zoo, the elephant may become very difficult for its new keeper to handle. Social hierarchies, although they may be relatively stable, are still susceptible to upheaval; obviously, a keeper in the dominant role would be in very serious danger if an elephant challenged him or her.

SOCIAL BEHAVIOR AND COMMUNICATION RESEARCH IN ZOOS

Other chapters in this volume discuss the logistics of research in zoos. What we wish to mention here is what can be done in the captive setting that cannot be done in the wild. In captivity, it is possible to get close to animals that may not be approachable in the wild. Animals may be unapproachable in the field because they cannot be habituated or because they are inaccessible, as with cliff nesters or canopy dwellers. In the case of animals that are difficult to habituate, such as canopy-dwelling primates, almost everything we know, until recently, has come from captive studies. In captivity it is also possible to explore quiet vocalizations and subtle visual signals or behaviors usually performed out of a field researcher's view.

The other benefit of research in captivity is the control available. It is possible to present specific foods and objects and to manipulate the social circumstances. Maples, Haraway, and Hutto (1989) took advantage of the creation of a siamang pair to study how vocal duetting developed. The likelihood of observing such an event in the wild would be very small. With the close and constant observation possible in a zoo, Maples et al. were able to document the development of the duet and why any particular duetting attempt failed. This is just one example of the unique contribution zoo researchers can make to the body of knowledge about animal communication and social behavior.

CONCLUSIONS

The management of wild mammals in captivity requires the consideration of a complex set of factors, including the maintenance of the proper social environment. Animal communication is a key element in the establishment of all mammalian social systems. Since many animal management problems have their origins in social behavior, it is recommended that communication mechanisms be considered when searching for answers to these problems. The animal's communication systems can also be important diagnostic tools for the captive animal manager, providing crucial information about both the animal's health and welfare and the keepers' safety.

REFERENCES

Adams, M. G. 1980. Odour-producing organs of mammals. *Symp. Zool. Soc. Lond.* 45:57–86.

Albone, E. S. 1984. *Mammalian semiochemistry: The investigation of chemical signals between mammals.* New York: John Wiley and Sons.

Bronson, F. H., and Macmillan, B. 1983. Hormonal responses to primer pheromones. In *Pheromones and reproduction in mammals,* ed. J. G. Vandenbergh, 175–97. New York: Academic Press.

Brown, C. H. 1989. The active space of blue monkey and grey-cheeked mangabey vocalizations. *Animal Behaviour* 37: 1023–34.

Brown, R. E., and Macdonald, D. W., eds. 1987. *Social odours in mammals.* 2 vols. New York: Oxford University Press.

Bullock, T., Orkand, R., and Grinnel, A. 1977. *Introduction to nervous systems.* San Francisco: W. H. Freeman.

Busnel, R. G., ed. 1963. *Acoustic behaviour of animals.* New York: Elsevier Publishing Company.

———. 1977. Acoustic communication. In *How animals communicate,* ed. T. A. Sebeok, 233–51. Bloomington: Indiana University Press.

Carlstead, K. 1991. Husbandry of the fennec fox, *Fennecus zerda:* Environmental conditions influencing stereotypic behaviour. *Int. Zoo Yrbk.* 30:202–7.

Clutton-Brock, T. H. 1979. The logical stag: Adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* 27: 211–25.

Conover, G. K., and Gittleman, J. L. 1989. Scent-marking in captive red pandas *(Ailurus fulgens). Zoo Biol.* 8:193–205.

Dixson, A. F. 1983. Observations on the evolution and behavioural significance of sexual skin in female primates. *Adv. Stud. Behav.* 13:63–106.

Dodd, G. H., and Squirrell, D. J. 1980. Structure and mechanism in the mammalian olfactory system. *Symp. Zool. Soc. Lond.* 45: 35–56.

Eisenberg, J. F. 1981. *The mammalian radiations: An analysis of trends in evolution, adaptation and behavior.* Chicago: University of Chicago Press.

Eisenberg, J. F., and Golani, I. 1977. Communication in Metatheria. In *How animals communicate,* ed. T. A. Sebeok, 575–99. Bloomington: Indiana University Press.

Eisenberg, J. F., and Gould, E. 1970. *The tenrecs: A study in mammalian behavior and evolution.* Smithsonian Contributions to Zoology, no. 27. Washington, D.C.: Smithsonian Institution Press.

Eisenberg, J. F., and Kleiman, D. G. 1972. Olfactory communication in mammals. *Annu. Rev. Ecol. Syst.* 3:1–31.

Epple, G. 1972. Social communication by olfactory signals in marmosets. *Int. Zoo Yrbk.* 13:36–42.

Erwin, J. 1986. Environments for captive propagation of primates: Interaction of social and physical factors. In *Primates: The road to self-sustaining populations,* ed. K. Benirschke, 297–306. Springer-Verlag, New York.

Ewer, R. F. 1968. *The ethology of mammals.* New York: Plenum Press.

———. 1973. *The carnivores.* Ithaca, N.Y.: Cornell University Press.

Fagen, R. 1981. *Animal play behavior.* New York: Oxford University Press.

Fay, R. R., and Popper, A. N. 1985. The octavolateralis system. In *Functional vertebrate morphology,* ed. M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, 291–316. Cambridge, Mass.: Harvard University Press.

Fentress, J. C., Fiels, R., and Parr, H. 1978. Social dynamics and communication. In *Behavior of captive wild animals,* ed. H. Markowitz and V. H. Stevens, 67–106. Chicago: Nelson-Hall.

Fossey, D. 1983. *Gorillas in the mist.* Boston: Houghton Mifflin Company.

Gautier, J. P., and Gautier, A. 1977. Communication in Old World monkeys. In *How animals communicate,* ed. T. A. Sebeok, 890–964. Bloomington: Indiana University Press.

Geldard, F. A. 1977. Tactile communication. In *How animals communicate,* ed. T. A. Sebeok, 211–32. Bloomington: Indiana University Press.

Glatston, A. R., Geilvoet-Soeteman, E., Hora-Pecek, E., and Hooff, J. A. R. A. M. van. 1984. The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, *Saguinus oedipus oedipus. Zoo Biol.* 3:241–53.

Goodall, J. 1986. *The chimpanzees of Gombe: Patterns of behavior.* Cambridge Mass.: Belknap Press of Harvard University Press.

Gosling, L. M. 1982. A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* 60:89–118.

Green, S., and Marler, P. 1979. The analysis of animal communication. In *Handbook of behavioral neurobiology,* vol. 3, ed. P. Marler and J. G. Vandenbergh, 73–157. New York: Plenum Press.

Hailman, J. P. 1977. *Optical signals.* Bloomington: Indiana University Press.

Halliday, T. R., and Slater, P., eds. 1983. *Animal behavior: Communication.* New York: W. H. Freeman.

Hearn, J. P., Abbott, D. H., Chambers, P. C., Hodges, J. K., and Lunn, S. F. 1978. Use of the common marmoset, *Callithrix jacchus,* in reproductive research. In *Primates in medicine,* vol. 10, 40. Basel: Karger.

Hooff, J. A. R. A. M. van. 1986. Behavioral requirements for self-sustaining primate populations: Some theoretical considerations and a closer look at social behavior. In *Primates: The road to self-sustaining populations,* ed. K. Benirschke, 307–19. New York: Springer-Verlag.

Hosey, G. R. 1989. Behavior of the Mayotte lemur, *Lemur fulvus mayottensis,* in captivity. *Zoo Biol.* 8:27–36.

Hutchins, M., and Barash, D. P. 1976. Grooming in primates: Implications for its utilitarian function. *Primates* 17:145–50.

Inglett, B. J., French, J. A., Simmons, L. G., and Vires, K. W. 1989. Dynamics of intrafamily aggression and social reintegration in lion tamarins. *Zoo Biol.* 8:67–78.

Johnson, R. P. 1973. Scent marking in mammals. *Anim. Behav.* 21:521–35.

Johnston, R. E. 1983. Chemical signals and reproduction behavior. In *Pheromones and reproduction in mammals,* ed. J. G. Vandenbergh, 3–38. New York: Academic Press.

Johnston, R. E., and Schmidt, T. 1979. Responses of hamsters to scent marks of different ages. *Behav. Neural Biol.* 26:64–75.

King, J. A. 1959. The social behavior of prairie dogs. *Sci. Am.* 10: 308–15.

Koontz, F. W. 1984. Sternal gland scent communication in the rufous elephant-shrew, *Elephantulus rufescens* Peters, with additional observations on behavior and reproduction in captivity. Ph.D. dissertation, University of Maryland.

Krebs, J. R., and Davies, N. B. 1993. *An introduction to behavioural ecology.* 3d ed. Boston: Blackwell.

Levine, J. S. 1985. The vertebrate eye. In *Functional vertebrate morphology,* ed. M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, 317–37. Cambridge Mass.: Harvard University Press.

Leyhausen, P. 1979. *Cat behavior: The predatory and social behavior of domestic and wild cats.* New York: Garland STPM Press.

Lorenz, K. Z. 1966. *On aggression.* London: Methuen.

Maple, T. L., and Finlay, T. W. 1986. Evaluation of the environment of captive nonhuman primates. In *Primates: The road to self-sustaining populations,* ed. K. Benirschke, 479–88. New York: Springer-Verlag.

———. 1989. Applied primatology in the modern zoo. *Zoo Biol.* suppl. 1:101–16.

Maples, E. G., Haraway, M. M., and Hutto, C. W. 1989. Development of coordinated singing in a newly formed siamang pair *(Hylobates syndactylus). Zoo Biol.* 8:367–78.

Morton, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules. In *Acoustic communication in birds,* vol. 1, ed. D. E. Kroodsma, E. H. Miller, and H. Ouellet, 183–212. New York: Academic Press.

Oppenheimer, J. R. 1977. Communication in New World monkeys. In *How animals communicate,* ed. T. A. Sebeok, 851–89. Bloomington: Indiana University Press.

Payne, K. B., Langbauer, W. R., and Thomas, E. M. 1986. Infrasonic calls of the Asian elephant *(Elephas maximus). Behav. Ecol. Sociobiol.* 18:297–301.

Piercy, J. E., and Embelton, T. F. W. 1977. Review of noise propagation in the atmosphere. *J. Acoust. Soc. Am.* 61:1404–18.

Poduschka, W. 1977. Insectivore communication. In *How animals communicate,* ed. T. A.Sebeok, 600–633. Bloomington: Indiana University Press.

Pola, Y. V., and Snowdon, C. T. 1975. The vocalizations of pygmy marmosets *(Cebuella pygmaea). Anim. Behav.* 23:826–42.

Poole, T. 1985. *Social behaviour in mammals.* New York: Chapman and Hall.

Quay, W. B. 1977. Structure and function of skin glands. In *Chemical signals in vertebrates,* ed. D. Müller-Schwarze and M. M. Mozell, 1–16. New York: Plenum Press.

Ralls, K. 1971. Mammalian scent marking. *Science* 171:443–49.

Regnier, F. E., and Goodwin, M. 1977. On the chemical and environmental modulation of pheromone release from vertebrate scent markers. In *Chemical signals in vertebrates,* ed. D. Müller-Schwarze and M. M. Mozell, 115–34. New York: Plenum Press.

Roberts, M., and Kohn, F. 1993. Habitat use, foraging behavior, and activity patterns in reproducing western tarsiers, *Tarsius bancanus,* in captivity: A management synthesis. *Zoo Biol.* 12: 217–32.

Roberts, M., Koontz, F., Phillips, L., and Maliniak, E. 1987. Management and biology of the prehensile-tailed porcupine, *Coendou prehensilis,* at Washington NZP and New York Zoological Park. *Int. Zoo Yrbk.* 26:265–75.

Roeper, N. J. 1981. Foot drumming in the elephant shrew, *Elephantulus rufescens.* M.S. thesis, University of Maryland.

Sales, G., and Pye, D. 1974. *Ultrasonic communication by animals.* London: Chapman and Hall.

Schleidt, W. M. 1973. Tonic communication: Continual effects of discrete signals in animal communication systems. *J. Theor. Biol.* 42:359–86.

Scott, J. P., and Fredericson, E. 1951. The causes of fighting in mice and rats. *Physiol. Zool.* 24 (4): 273–309.

Sebeok, T. A. ed. 1968. *Animal communication.* Bloomington: Indiana University Press.

———. 1972. *Perspectives in zoosemiotics.* The Hague: Mouton.

———, ed. 1977. *How animals communicate.* Bloomington: Indiana University Press.

Shirley, S. G. 1984. Mammalian chemoreception. In *Mammalian semiochemistry: The investigation of chemical signals between mammals,* ed. E. S. Albone, 243–77. New York: John Wiley and Sons.

Slater, P. J. B. 1985. *An introduction to ethology.* New York: Cambridge University Press.

Smith, W. J. 1977. *The behavior of communication.* Cambridge Mass.: Harvard University Press.

Snowdon, C. T. 1989. The criteria for successful captive propagation of endangered primates. *Zoo Biol.* suppl. 1:149–61.

Sokolov, V. E. 1982. *Mammal skin.* Berkeley: University of California Press.

Suomi, S. J. 1986. Behavioral aspects of successful reproduction in primates. In *Primates: The road to self-sustaining populations,* ed. K. Benirschke, 331–40. New York: Springer-Verlag.

Tembrock, G. 1989. Biocommunication in mammals with special references to acoustic signals. *Int. J. Mammal. Biol.* 54:65–80.

Tenaza, R. R. 1989. Female sexual swellings in the Asian colobine *Simias concolor. Am. J. Primatol.* 17:81–86.

Thompson, K. V. 1993. Aggressive behavior and dominance hierarchies in female sable antelope, *Hippotragus niger:* Implications for captive management. *Zoo Biol.* 12:189–202.

Waal, F. B. M. de. 1987. Dynamics of social relationships. In *Primate societies,* ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, 421–30. Chicago: University of Chicago Press.

Walther, F. R. 1984. *Communication and expression in hoofed mammals.* Bloomington: Indiana University Press.

Wellington, J. L., Beauchamp, G. K., and Wojciechowski-Metzler, C. 1983. Stability of chemical communicants in urine: Individual identity and age of sample. *J. Chem. Ecol.* 9:235–45.

Wiley, R. H. 1983. The evolution of communication: Information and manipulation. In *Animal behaviour: Communication,* ed. T. R. Halliday and P. J. B. Slater, 156–89. New York: W. H. Freeman.

Wiley, R. H., and Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3: 69–94.

Wilson, E. O. 1968. Chemical systems. In *Animal communication,* ed. T. A. Sebeok, 75–102. Bloomington: Indiana University Press.

———. 1972. Animal communication. *Sci. Am.* 227 (3): 52–60.

———. 1975. *Sociobiology: The new synthesis.* Cambridge, Mass.: Harvard University Press.

Wilson, E. O., and Bossert, W. H. 1963. Chemical communication among animals. *Rec. Prog. Horm. Res.* 19:673–716.

33

Mammalian Social Organization and Mating Systems

JOEL BERGER AND ELIZABETH F. STEVENS

Wild animals have been maintained in confinement for more than 5,000 years, yet study of their social organization is relatively recent (for reviews see Fisler 1969; Eisenberg 1966, 1981; Clutton-Brock and Harvey 1977; Kleiman 1977; Gosling and Petrie 1981; Smuts et al. 1987). It is now evident that the long-term maintenance of a captive population requires understanding and consideration of the species' social behavior and its mating system. Unfortunately, details about the social organization of many species are unknown. As conservation continues to emerge as a prominent theme for the twenty-first century, managers of animal populations increasingly will require knowledge of animal social organization and mating systems. The purpose of this chapter, therefore, is to summarize how knowledge of mammalian social systems can be applied to the captive situation. This chapter is organized into three sections: (1) a description of the patterns of social organization and mating systems; (2) a discussion of the ecological constraints on social organization; and (3) a discussion of the flexibility of social organization and considerations to be taken into account when forming captive social groups.

PATTERNS OF SOCIAL ORGANIZATION AND MATING SYSTEMS

Various definitions of social organization and mating systems exist (Brown and Orians 1970; Wilson 1975; Wittenberger 1981; Michener 1983; Shields 1987). One simple categorization system uses grouping patterns, the results of a species' dispersion in space and time (Eisenberg 1981). Thus, a working definition of social organization is the modal grouping pattern of a species. Social organization can be most simply categorized as either solitary or social. Examples of social organization patterns include solitary species, family groups, female kin groups, single-male groups, and multimale groups.

Definitions of mating systems use both the contributions made by the sexes to the gene pool and the breeding tactics of each sex. Mammalian mating systems can be most simply broken down into four categories: monogamous, polygynous, polyandrous, and promiscuous. The principal problem in defining these systems is identifying the extent to which males and females form bonds and the time period over which these bonds extend (Kleiman 1977; Wittenberger and Tilson 1980). The best definitions of mating systems rely on criteria related to genetic contributions (see Trivers 1972; Kleiman 1977; Emlen and Oring 1977), although data on copulation frequencies with different partners are often substituted when data on genetic contributions are lacking.

Solitary species are those in which animals are most frequently found by themselves. This is not to say that individuals never contact one another; obviously they must if reproduction occurs. But, relative to animals with other types of social organization, members of solitary species are alone most of the time. Ring-tailed cats, *Bassariscus astutus*, lesser mouse lemurs, *Microcebus murinus*, and giant pandas, *Ailuropoda melanoleuca*, are all considered solitary species.

Family groups are composed of one adult male, one adult female, and their offspring from one or more litters. The golden lion tamarin, *Leontopithecus rosalia*, is a species with a typical family group social organization. Family groups can be further subdivided into (1) pairs or temporary families, (2) nuclear families, which may include subadults, and (3) extended families, which include related but nonbreeding adults (Kleiman 1980).

Female kin groups are associations of related females not defended by males. Usually, dispersal of males from their natal groups results in groups containing only females. Males live alone or in small bachelor groups and join the female kin groups only during the breeding season. Female kin groups tend to be established along matrilines. Individual females may be somewhat spatially clumped, as in elephants and several ungulates, such as bighorn sheep, *Ovis canadensis*, and American bison, *Bison bison;* or they may be more widely dispersed but still live in proximity to one another, as in several rodents, including Belding's ground squirrels, *Spermophilus beldingi,* and white-tailed prairie dogs, *Cynomys leucurus.*

Single-male groups consist of a single adult male, two or more adult females (who can be related or unrelated), and often their young. Examples of species with single-male groups include drills, *Mandrillus leucophaeus,* and mandrills, *Mandrillus sphinx* (Schaaf 1990). In Burchell's zebras, *Equus burchellii,* Przewalski's horses, *E. przewalskii,* and feral horses, *E. caballus* (Berger 1986; Stevens 1990), these groups are called bands; in hamadryas baboons, *Papio hamadryas,* they are troops (Kummer 1968); and in black-tailed prairie dogs, *Cynomys ludovicianus,* they are coteries (King 1955; Hoogland 1982). For some species, the term "harem" is used to refer to the females in single-male groups. Males of some species defend harems year-round, as in zebras, impalas, *Aepyceros melampus,* and gorillas, *Gorilla gorilla.* Males of other species defend harems only during the breeding season, as in red deer, *Cervus elaphus,* and elephant seals, *Mirounga* spp.; in this case the sexes are segregated throughout much of the year. In species with single-male groups, juvenile males leave their natal groups and often associate with other males in bachelor groups. Adult males not associating with females are functionally bachelors, as they rarely contribute to the breeding. Adult bachelors are either loosely associated with bachelor groups or live solitarily.

Multimale groups contain two or more breeding adults of both sexes and young. This classification has been used mostly for primates such as red colobus monkeys, *Procolobus badius,* and mantled howler monkeys, *Alouatta villosa* (Struhsaker 1975; Eisenberg 1981), but other taxa (e.g., rock hyraxes, *Procavia johnstoni*) could rightfully be included in this category. African lions, *Panthera leo,* dwarf mongooses, *Helogale parvula,* and banded mongooses, *Mungos mungo,* are additional examples, although their groupings are known as prides and packs respectively (Schaller 1972; Rood 1983, 1986, 1987).

Within these different social organizations the mating system can be monogamous, polygynous, polyandrous, or promiscuous. *Monogamy* occurs when each individual mates exclusively with a single individual from the opposite sex, presumably over a substantial portion of their lifetimes (Kleiman 1977). While monogamy is practically the rule in birds, in which males participate equally in parental care, it is rare among mammals, in which males participate very little (if at all) in parental care. Monogamy occurs in about 3% of mammals, and paternal care is most common in those species that mate monogamously (Kleiman and Malcolm 1981). Two basic types of monogamy have been described: *facultative* and *obligate* (Kleiman 1977). Facultative monogamy occurs where food resources are widely distributed. The sexes coexist on one territory, sometimes protecting a common resource (e.g., rufous elephant shrews, *Elephantulus rufescens:* Rathbun 1979). Species that are facultatively monogamous may vary in their degree of association with mates, and it is suspected that in the wild they may sometimes become polygynous (Malcolm 1985; Moehlman 1986). On the other hand, species characterized by obligate monogamy are those in which two parents typically are necessary for the successful rearing of young. Males and females are often seen together, and far less social and ecological flexibility is presumed to occur than in facultatively monogamous species (Kleiman 1977; Eisenberg 1981). Canids such as coyotes, *Canis latrans,* and silver-backed jackals, *C. mesomelas,* are examples of species in which pup survivorship is improved when males share parental responsibilities (Moehlman 1983; Bekoff and Wells 1986).

Polygyny, in which males breed with more than one female during a single breeding season and often have no parental care responsibilities, characterizes the majority of mammalian species. Polygynous systems typically involve one male defending a group of females. In contrast is *polyandry,* in which females breed with more than one male, but some males mate with only one female (Thornhill and Alcock 1983). Only a few polyandrous mammal species exist (Kleiman 1977; Wittenberger and Tilson 1980; Eisenberg 1981). Large canids such as the Asiatic wild dog, *Cuon alpinus,* African wild dog, *Lycaon pictus,* and gray wolf, *Canis lupus,* show indications of polyandry (Moehlman 1986).

Promiscuity is characterized by the absence of any pair bond or long-term relationship between the male and the female. In general, promiscuous mating systems occur in species in which males and females come together only for mating. A common promiscuous system, seen in many desert and grassland rodent species, involves a single male occupying a large range and mating with any female in estrus with which he comes in contact. The male and female part shortly after mating.

A very specialized and unusual type of mating system is *lekking.* Leks are areas where males concentrate to attract and copulate with females. Males defend very small individual territories on the lek. Females derive no material benefits from visiting leks because they are rarely, if ever, situated at or adjacent to food sources (Wittenberger 1981; Bradbury and Gibson 1983). Lekking occurs among hammer-headed bats, *Hypsignathus monstrosus* (Bradbury 1977), and several African antelopes, including the Uganda kob, *Kobus kob,* lechwe, *K. leche,* and topi, *Damaliscus korrigum;* among the latter two species, up to 100 males may congregate at a lek (Buechner and Schloeth 1965; Gosling 1986).

Table 33.1 gives selected examples of species kept in captivity, showing their different types of mating systems and social organization.

ECOLOGY AND CONSTRAINTS ON SOCIAL ORGANIZATION

Patterns of mammalian social organization have evolved in concert with, and in response to, ecological conditions. It is widely accepted that social behavior evolves as an adaptation to maximize individual fitness in the face of two main types of ecological pressures: predation pressure and resource distribution (Wrangham and Rubenstein 1986; Alexander 1974). Using a comparative approach, classic studies of ungulates (Jarman 1974; Geist 1974) and primates (Crook and Gartlan 1966; Clutton-Brock 1974) have shown that social groupings in related species vary

TABLE 33.1. Representative Species of Different Orders Varying in Social Organization and Mating Systems

Species	Social Organization	Mating System
Marsupials		
Antechinus (*Antechinus stuartii*)	SS	PA?
American possum (*Didelphis virginiana*)	SS	PA?
Leadbeater's possum (*Gymnobelideus leadbeateri*)	FG	M
Tasmanian barred bandicoot (*Perameles gunnii*)	SS	PO
Sugar glider (*Petaurus breviceps*)	FG	PO
Matschie's tree kangaroo (*Dendrolagus matschiei*)	?	PR
Red kangaroo (*Macropus rufus*)	?	PR
Insectivores		
Solenodon (*Solenodon paradoxus*)	SS	M?
Hedgehog (*Atelerix albiventris*)	SS	M?
Microgale (*Microgale dobsoni*)	SS	M?
Bats		
Hammerhead bat (*Hypsignathus monstrosus*)	OM	PO, L
Leaf-nosed bat (*Phyllostomus hastatus*)	OM	PO
Red bat (*Lasiurus borealis*)	SS	?
Primates		
Common marmoset (*Callithrix jacchus*)	FG	M
Golden lion tamarin (*Leontopithecus rosalia*)	FG	M
Titi monkey (*Callicebus moloch*)	FG	M
Kloss's gibbon (*Hylobates klossii*)	FG	M
Patas monkey (*Erythrocebus patas*)	OM	PO
Gorilla (*Gorilla gorilla*)	MM	PO
Orangutan (*Pongo pygmaeus*)	SS	PO?
Ring-tailed lemur (*Lemur catta*)	MM	PO?
Yellow baboon (*Papio cynocephalus*)	MM	PO
Crowned guenon (*Cercopithecus pogonias*)	OM	PO
Red colobus (*Procolobus badius*)	MM	PO
Rodents		
Hoary marmot (*Marmota caligata*)	FG	M
Yellow-bellied marmot (*Marmota flaviventris*)	OM	PO
Ground hog (*Marmota monax*)	SS	PO?
Grasshopper mouse (*Onychomys leucogaster*)	FG	M?
Deer mouse (*Peromyscus maniculatus*)	SS, FG	PO, M?
Beaver (*Castor canadensis*)	FG	M
Arctic ground squirrel (*Spermophilus parryii*)	FK	PO
Columbian ground squirrel (*Spermophilus columbianus*)	FK	PO
Mara (*Dolichotis* spp.)	FG	M
Carnivores		
African wild dog (*Lycaon pictus*)	MM	M
Gray wolf (*Canis lupus*)	FG	M
Bat-eared fox (*Otocyon megalotis*)	FG, SS	M
Dwarf mongoose (*Helogale parvula*)	FG, OM	M
Spotted hyena (*Crocuta crocuta*)	MM	PO
Ring-tailed cat (*Bassariscus astutus*)	SS	?
African lion (*Panthera leo*)	MM, OM	PO
Tiger (*Panthera tigris*)	SS	PO
Jaguar (*Panthera onca*)	SS	PO
Cheetah (*Acinonyx jubatus*)	SS	PO
Grizzly bear (*Ursus arctos*)	SS	PO
European polecat (*Mustela putorius*)	SS	PR
Ungulates		
Dik-dik (*Madoqua kirkii*)	FG	M
Klipspringer (*Oreotragus oreotragus*)	FG	M
Nilgiri tahr (*Hemitragus hylocrius*)	SE	PO
African buffalo (*Syncerus caffer*)	SE	PO
Red deer (*Cervus elaphus*)	SE	PO
Collared peccary (*Pecari tajacu*)	MM	PO?
Guanaco (*Lama guanicoe*)	OM	PO
Burchell's zebra (*Equus burchellii*)	OM	PO
Grevy's zebra (*Equus grevyi*)	?	PO

Source: Adapted from Clutton-Brock and Harvey 1977; Collins, Busse, and Goodall 1984; Eisenberg 1981; Kleiman 1977; Michener 1983; Smuts et al. 1987; and Macdonald 1984.

Note: Abbreviations: SS, solitary species; OM, one-male groups; MM, multimale groups; FG, family groups; FK, female kin groups; SE, sexually segregated groups; L, leks; M, monogamy; ?, classification difficult; PO, polygyny; PA, polyandry; PR, promiscuous.

according to resource distribution and predator pressure. Long-term studies have demonstrated the intricate interaction of ecological, social, demographic, and developmental constraints on social systems (Clutton-Brock 1974; Dunbar 1984; Rubenstein and Wrangham 1986; Clutton-Brock 1988).

Predation Pressure and Resource Distribution

Mammalian species have evolved a number of strategies for avoiding predators. Hiding is a practical strategy for smaller species, especially those not living in large groups. Group living can also reduce predator pressure (Hamilton 1971). By living in a large group, an individual reduces the chances that it will be the one caught by a predator, that is, it takes advantage of the difference between being one of twenty versus one of two. Predator avoidance, however, is not the only factor responsible for social organization. The distribution of resources, particularly of food, water, and shelter, plays an equally important role. It is unlikely, for example, that large groups of animals will form if food sources are widely and unevenly distributed.

Jarman's (1974) classic study of ungulates illustrates these points. Species such as duikers, *Cephalophus* spp., that live in thick vegetation and forage on leaves and berries form monogamous pair-bonds and live on exclusive territories. In antelopes that live at the forest edge and in grassland, such as impalas and Thomson's gazelles, *Gazella thomsonii,* males defend territories with lush forage that attract herds of females. These territorial males defend the females inside their territories for as long as possible and mate with any females in estrus. In contrast, African buffalo, *Syncerus caffer,* eat grass and migrate on the open savanna. Buffalo live in large mixed-sex herds in which the males have formed a dominance hierarchy. The alpha males form "tending bonds" with females in estrus. Beta males mate only when two or more females are in estrus simultaneously.

Size and Morphology

Size and morphology also influence how a species responds to ecological pressures—how it maximizes nutrient intake and avoids predators. An insectivore such as the solenodon, *Solenodon* spp., and a comparably sized herbivore like the pika, *Ochotona princeps,* might both hone their activity patterns in response to potential predation or to maximize nutrient intake, but because the morphology and nutritional demands of the two species differ dramatically, we would not expect them to exhibit similar mating systems. Pikas are apparently monogamous (Smith and Ivins 1983), while solenodons appear to be polygynous (Eisenberg and Gould 1966). In primates, several trends emerge when body size, activity patterns, grouping, and foraging patterns are considered (Clutton-Brock and Harvey 1977). Nocturnal species tend to be smaller than diurnal ones, possibly because smaller species are likely to be better concealed from predators and because they may travel more effectively over smaller branches and twigs (Clutton-Brock and Harvey 1977). Also, folivores (mature-leaf specialists) have smaller home ranges, spend more time feeding, and cover less distance per day than frugivorous primates.

Referring again to Jarman's (1974) comparative study of ungulate social organization, size and morphology patterns were also evident. The smaller species, like the duikers and Kirk's dik-dik, *Madoqua kirkii,* live in thick vegetation, avoid predators by hiding, and have a monogamous mating system. The medium-sized impalas and gazelles defend territories, find safety in numbers while foraging, and have a polygynous mating system. The very largest bovids live in large migratory herds, thereby finding safety in numbers, and have a polygynous mating system based on male dominance hierarchies.

Competition for Mates

The spatial and temporal distribution of another resource, potential mates, also influences social organization and mating systems. In the 3% of mammal species that are monogamous, the sex ratio of breeding adults is 1:1, and the competition for mates is not as keen as it is in polygynous species, in which the sex ratio of breeding adults is skewed heavily toward females.

In the majority of mammal species, males have no parental care duties. A male's reproductive success is, therefore, directly related to the number of females he can inseminate, which, in turn, is related to the distribution of females. The distribution of females is determined by the distribution of food resources and predators. Emlen and Oring (1977) formalized a model of mating systems based on these ecological constraints. They proposed two distinct types of polygynous mating systems based on the degree to which either multiple mates or resources critical to gaining multiple mates are economically defensible: (1) resource defense polygyny, in which males defend resources essential to females, and (2) female defense polygyny, in which males directly defend females. When resources are so sparsely distributed that they are not defensible, males defend females directly instead.

Examples of resource defense polygyny in mammals include species in which males defend resources attractive to females and then defend the females attracted to those territories. This is the case for most of the bovids (Owen-Smith 1977; Spinage 1986). Two camelids, the vicuña, *Vicugna vicugna* (Franklin 1974), and the guanaco, *Lama guanicoe* (Franklin 1974), defend harems on their territories year-round, as do members of the order Hyracoidea (rock hyrax, *Procavia* spp., and bush hyrax, *Heterohyrax* spp.) (Hoeck, Klein, and Hoeck 1982). Another territorial harem holder is a sciurid, the yellow-bellied marmot, *Marmota flaviventris* (Downhower and Armitage 1971; Armitage 1986), which defends a territory containing the burrows of one or more females. In all these territorial harem-holding species, changes in the abundance and distribution of resources would affect not only spacing among females but also the number of females that a male's territory could support. Elephant seals and gray seals, *Halichoerus grypus,* patrol territories on beaches where females gather to give birth and then mate (Le Boeuf 1974). In elephant seals, male reproductive success is dependent upon the ability to accumulate fat reserves during the nonbreeding season to facilitate guarding a territory and fighting with other males.

Female defense polygyny, which can be seasonal or year-round, occurs when males defend females directly and do not defend territories. Single-male units may move about together to find resources. In red deer, males defend harems only during the rut. As with elephant seals, male reproductive success is dependent upon accumulating fat reserves so that males can concentrate their efforts on defending females during the rut. In contrast, males of some of the equids and primate species defend harems year-round. In feral horses and Burchell's zebras, males defend harems during both the breeding season and the nonbreeding season. The same holds true for some of the cercopithecine primates—the hamadryas baboon, *Papio hamadryas,* the gelada baboon, *Theropithecus gelada,* and the patas monkey, *Erythrocebus patas*— as well as for gorillas. Harem stability in these species is maintained by the male's behavior toward females and intruding males.

Promiscuous mating systems can occur in both solitary and social species. In elephants, males live solitarily while females live in large female kin groups. Females are in estrus for only a few days at a time, so the distribution of sexually receptive cows is constantly changing in space and time. Bulls travel long distances to monitor the reproductive status of the cows in their home ranges. When a male finds a receptive female, he must compete with other males for the mating opportunity. Males stay with a female kin group for a few days at the most (Moss 1975).

CAPITALIZING ON THE FLEXIBILITY OF SOCIAL ORGANIZATION: CONSIDERATIONS WHEN FORMING CAPTIVE SOCIAL GROUPS

Variability from year to year, or season to season, in resource abundance and distribution, as well as in demographic parameters like population density and age structure, can affect mammal social organization. One of the best early demonstrations that the distribution of food, acting in conjunction with population density, mediates shifts in social organization stems from Kinsey's (1971) experimental work on wood rats, *Neotoma fuscipes.* Wood rats shifted from a system in which males defended territories to a strict dominance hierarchy as density increased. Other analyses of spacing have also shown that males of some territorial species will abandon resource defense when food is above or below certain threshold levels (Lott 1984).

The distribution of food is probably the key ecological constraint on species classified as facultatively monogamous. These species may vary in their degree of association with mates, and it is suspected that in the wild they may sometimes become polygynous (Malcolm 1985; Moehlman 1986). Dik-diks, for example, are probably facultatively monogamous. Males are not known to contribute any direct parental care, but because the food source is evenly, but widely, dispersed, it is likely that it would not be economically feasible for a male to defend a territory large enough to accommodate two females. In captivity, where food sources are plentiful, more than one female has been placed with a single male with no deleterious effects (Kleiman 1980).

The same concept is applicable to orangutans, *Pongo pygmaeus,* another species socially constrained by the distribution of food (Maple 1980). Due to their large size and their need to consume large quantities of food, orangutans cover a large area each day while foraging. Their solitary social organization is probably attributable to the fact that it would be impossible for males to defend food resources or females given how widely dispersed the food is. In captivity, orangutans are commonly housed in single-male social units with great success. They appear to be quite social when food sources are abundant.

Changes in demographic parameters such as age structure and sex ratio can also act as important determinants of social organization. In pronghorns, *Antilocapra americana,* traditionally a territorial species in the enclosed 20,000-acre National Bison Range, the social organization shifted to one of harem defense after a catastrophic winter die-off of older males (Byers and Kitchen 1988). In feral horses, when the sex ratio of mature males to mature females was even or weighted toward males, many single-male bands became multimale bands (Stevens 1987) as males sought different strategies for acquiring harems.

The major ecological constraints on social organization in the wild—distribution of food resources, predation pressure, and distribution of potential mates—are all regulated in the captive situation. Adequate, if not plentiful, food resources are constantly and easily available. Predators and potential prey animals are not housed together. Depending upon the breeding priorities for a particular species, individual animals are given access to potential mates under controlled circumstances. Given this control, the manager of captive animals strives to create the most appropriate social environment for each species.

What Kind of Social Group Is Appropriate in Captivity?

For those species classified as solitary, individuals are normally held in separate enclosures. Males and females are allowed access to each other only when the females are sexually receptive. This is the case for many of the solitary carnivores. In the case of giant pandas, known to be a solitary species, the male and female at the National Zoo were kept in adjacent enclosures, and for a few hours each day the door between the enclosures was opened so that they could choose to be together or to remain in their respective enclosures. Of course, if breeding is not a priority, then males and females can be kept separately year-round. Many carnivores, including tigers and bears, can be kept together in groups of the same sex, and even in pairs when contraception is available.

For social species, the first step in determining the appropriate social grouping in captivity is to find out what the species' social organization is in the wild. The next step is to decide whether or not breeding is a priority. If breeding is not desired, then either contraception has to be considered, or males cannot be kept with females. In either case, Wemmer and Fleming (1975) suggest that when developing groups of unfamiliar individuals, it is best to begin with a single pair so that social relationships can be clearly established.

Consider first the situation in which breeding is a priority. Family groups can be started by pairing a male and a female and then letting their offspring remain with them. Female kin groups and single-male groups do not differ operationally very much from one another in captivity. For those species that naturally form female kin groups, there will often not be enough kin available to form such a group in captivity, and a group will most likely have to be formed with some unrelated females mixed in. Multimale groups are less common in captivity than they are in the wild, mostly due to the fact that these groups are normally very large and occupy a tremendous amount of space, which is difficult to emulate in zoos. In general, managers have found that related males are more tolerant of each other in multimale groups than are unrelated males. Furthermore, when breeding is a priority, multimale groups may be impractical because of the need to determine and regulate paternity. Despite the fact that technological advances now make it possible to determine paternity from blood and tissue samples, most managers want to ensure that only particular males have breeding opportunities.

In situations in which breeding is not desired, the alternatives are the same for social species as for solitary species: males and females must be housed separately, or, if they are housed together, contraception must be employed. The problem of extra males is prevalent among mammals in zoos. Additional males (that is, additional to the one male housed in a single-male unit) can often be kept in bachelor groups or housed individually; bachelor groups have been formed with ruffed lemurs, *Varecia variegata,* small-clawed otters, *Amblonyx cinereus,* dwarf mongooses, meerkats, *Suricata suricatta,* cheetahs, *Acinonyx jubatus,* and gerenuks, *Litocranius walleri.* However, bachelor groups are sometimes only temporary solutions. Bachelorhood is a common phenomenon in those mammal species in which young males disperse from their natal groups (which includes most mammal species). Until males are sexually and developmentally mature, they may spend time in bachelor groups. In the wild, adult males sometimes split off from bachelor groups. Extra adult males in captivity that are not compatible with bachelor groups must be housed alone.

The formation of leks in captivity for species that naturally form leks has not yet been attempted. It would undoubtedly require considerable space and would probably involve a fair amount of aggression between males, a risk that animal managers are usually reluctant to take.

CONCLUSIONS

In recent years great strides have been made in the study of mammal social organization and mating systems, as well as in the application of such studies to the management of captive species. Understanding the patterns of social organization and the ecological pressures that influence social organization and mating systems in the wild is essential to successful captive animal management.

The beauty of animal social organization is that it is sensitive to so many environmental and ecological factors; there are not, in general, any hard-and-fast rules for each species because of these intricate links with the social and physical environment. There are, however, patterns for each species. The challenge that lies ahead for animal managers is to stay abreast of studies in natural ecosystems so that they can make better decisions about managing the social and physical environments of the animals in their care.

REFERENCES

Alexander, R. D. 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5:325–83.

Armitage, K. B. 1986. Marmot polygyny revisited: Determinants of male and female reproductive strategies. In *Ecological aspects of social evolution,* ed. D. I. Rubenstein and R. W. Wrangham, 303–31. Princeton, N.J.: Princeton University Press.

Bekoff, M., and Wells, M. C. 1986. Social ecology and behavior of coyotes. *Adv. Stud. Behav.* 16:251–338.

Berger, J. 1986. *Wild horses of the Great Basin: Social competition and population size.* Chicago: University of Chicago Press.

Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. *J. Zool.* (Lond.) 177:463–82.

Boggess, J. 1984. Infant killing and male reproductive strategies in langurs *(Presbytis entellus).* In *Infanticide: Comparative and evolutionary perspectives,* ed. G. Hausfater, and S. B. Hrdy, 283–310. New York: Aldine.

Bradbury, J. W. 1977. Lek mating behavior in the hammerhead bat. *Z. Tierpsychol.* 45:225–55.

Bradbury, J. W., and Gibson, R. M. 1983. Leks and mate choice. In *Mate choice,* ed. P. P. G. Bateson, 109–38. Cambridge: Cambridge University Press.

Brooks, R. J. 1984. Causes and consequences of infanticide in populations of rodents. In *Infanticide: Comparative and evolutionary perspectives,* ed. G. Hausfater and S. B. Hrdy, 331–48. New York: Aldine.

Brown, J. L., and Orians, G. H. 1970. Spacing patterns in mobile animals. *Annu. Rev. Ecol. Syst.* 1:239–62.

Buechner, H. K., and Schloeth, R. 1965. Ceremonial mating behavior in Uganda kob (*Adenota kob thomasi* Neumann). *Z. Tierpsychol.* 22:209–25.

Busher, P. E., and Jenkins, S. H. 1985. Behavioral patterns of a beaver family in California. *Biol. Behav.* 10:41–54.

Byers, J. A., and Kitchen, D. 1988. Mating system shift in pronghorn. *Behav. Ecol. Sociobiol.* 22:355–60.

Clutton-Brock, T. H. 1974. Primate social organization and ecology. *Nature* 250:539–42.

———, ed. 1988. *Reproductive success: Studies of individual variation in contrasting breeding systems.* Chicago and London: University of Chicago Press.

Clutton-Brock, T. H., and Harvey, P. H. 1977. Primate ecology and social organization. *J. Zool.* (Lond.) 183:1–39.

Collins, D. A., Busse, C. D., and Goodall, J. 1984. Infanticide in two populations of savannah baboons. In *Infanticide: Comparative and evolutionary perspectives,* ed. G. Hausfater and S. B. Hrdy, 193–216. New York: Aldine.

Crook, J. H., and Gartlan, J. S. 1966. Evolution of primate societies. *Nature* 210:1200–1203.

Downhower, J. F., and Armitage, K. B. 1971. The yellow-bellied marmot and the evolution of polygyny. *Am. Nat.* 105:355–70.

Dunbar, R. I. M. 1984. *Reproductive decisions.* Princeton, N.J.: Princeton University Press.

Eisenberg, J. F. 1966. The social organization of mammals. *Handb. Zool.,* Band 8, Lieferung 39:1–92.

———. 1981. *The mammalian radiations: An analysis of trends in evolution, adaptation, and behavior.* Chicago: University of Chicago Press.

Eisenberg, J. F., and Gould, E. 1966. The behavior of *Solenodon paradoxus* in captivity with comments on the behavior of other Insectivora. *Zoologica* 51:49–58.

Elwood, R. W., and Ostermeyer, M. C. 1984. Infanticide by male and female Mongolian gerbils: Ontogeny, causation, and function. In *Infanticide: Comparative and evolutionary perspectives,* ed. G. Hausfater and S. B. Hrdy, 367–86. New York: Aldine.

Emlen, S. T., and Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–23.

Estes, R. D., and Goddard, J. 1967. Prey selection and hunting behavior of the African wild dog. *J. Wildl. Mgmt.* 31:52–69.

Fisler, G. F. 1969. Mammalian organization systems. *Los Angeles Co. Mus. Publ.* 167:1–32.

Franklin, W. L. 1974. Camels and llamas. In *The encyclopedia of mammals,* ed. D. Macdonald, 512–15. New York: Facts on File Publications.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. *Am. Zool.* 14:205–20.

Gosling, L. M. 1986. The evolution of the mating strategies in male antelopes. In *Ecological aspects of social evolution,* ed. D. I. Rubenstein and R. W. Wrangham, 244–81. Princeton, N.J.: Princeton University Press.

Gosling, L. M., and Petrie, M. 1981. The economics of social organization. In *Physiological ecology,* ed. C. R. Townsend and P. Calow, 315–45. Oxford: Blackwell.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:295–311.

Hausfater, G., and Hrdy, S. B., eds. 1984. *Infanticide: Comparative and evolutionary perspectives.* New York: Aldine.

Hoage, R. J. 1977. Parental care in *Leontopithecus rosalia:* Sex and age differences in carrying behavior and the role of prior experience. In *Biology and conservation of the Callitrichidae,* ed. D. G. Kleiman, 293–305. Washington, D.C.: Smithsonian Institution Press.

Hoeck, H. N., Klein, H., and Hoeck, P. 1982. Flexible social organization in hyrax. *Z. Tierpsychol.* 59:265–98.

Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. *Science* 215:1639–41.

———. 1985. Infanticide in prairie dogs: Lactating females kill offspring of close kin. *Science* 230:1037–40.

Huck, U. W. 1984. Infanticide and the evolution of pregnancy block in rodents. In *Infanticide: Comparative and evolutionary perspectives,* ed. G. Hausfater and S. B. Hrdy, 349–66. New York: Aldine.

Jantschke, F. 1973. On the breeding and rearing of bush dogs, *Speothos venaticus,* at Frankfurt Zoo. *Int. Zoo Yrbk.* 13:141–43.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 58:215–67.

King, J. A. 1955. *Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota.* Contrib. Lab. Vert. Biol., Univ. Michigan. Ann Arbor. 67:1-123.

Kinsey, K. P. 1971. Social organization in a laboratory colony of wood rats *(Neotoma fuscipes).* In *Behavior and environment,* ed. A. H. Esser, 40–46. New York: Plenum.

Kleiman, D. G. 1977. Monogamy in mammals. *Q. Rev. Biol.* 52:39–69.

———. 1980. The sociobiology of captive propagation. In *Conservation biology: An evolutionary-ecological perspective,* ed. M. E. Soulé and B. A. Wilcox, 243–61. Sunderland, Mass.: Sinauer Associates.

Kleiman, D. G., and Malcolm, J. R. 1981. The evolution of male parental investment in mammals. In *Parental care in mammals,* ed. D. J. Gubernick and P. H. Klopfer, 347–87. New York: Plenum.

Kummer, H. 1968. *Social behavior of Hamadryas baboons.* Chicago: University of Chicago Press.

Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *Am. Zool.* 14:163–76.

Lott, D. F. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266–325.

Macdonald, D. 1984. *The encyclopedia of mammals.* New York: Facts on File Publications.

Malcolm, J. R. 1985. Paternal care in canids. *Am. Zool.* 25:853–56.

Maple, T. L. 1980. *Orang-utan behavior.* New York: Van Nostrand.

Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In *Recent advances in the study of mammalian behavior,* ed. J. F. Eisenberg and D. G. Kleiman, 528–72. Special Publication no. 7. Lawrence, Kans.: American Society of Mammalogists.

Moehlman, P. D. 1983. Socioecology of silverbacked and golden jackals *(Canis mesomelas* and *C. aureus).* In *Recent advances in the study of mammalian behavior,* ed. J. F. Eisenberg and D. G. Kleiman, 423–53. Special Publication no. 7. Lawrence, Kans.: American Society of Mammalogists.

———. 1986. Ecology of cooperation in canids. In *Ecological aspects of social evolution,* ed. D. I. Rubenstein and R. W. Wrangham, 64–86. Princeton, N.J.: Princeton University Press.

Moss, C. 1975. *Portraits in the wild.* London: Hamish Hamilton Ltd.

Owen-Smith, N. 1977. On territoriality in ungulates and an evolutionary model. *Q. Rev. Biol.* 52:1–38.

Penzhorn, B. L. 1985. Reproductive characteristics of a free-ranging population of cape mountain zebras. *J. Reprod. Fertil.* 73:51–57.

Pereira, M. E. 1983. Abortion following the immigration of an adult male baboon *(Papio cynocephalus). Am. J. Primatol.* 4:93–98.

Polis, G. A., Myers, C. A., and Hess, W. R. 1984. A survey of intraspecific predation within the class Mammalia. *Mammal Rev.* 4:187–98.

Rathbun, G. B. 1979. The social structure and ecology of elephant-shrews. *Beih. zur Z. Tierpsychol.* 20:1–77.

Rood, J. P. 1983. The social system of the dwarf mongoose. In *Recent advances in the study of mammalian behavior*, eds. J. F. Eisenberg, and D. G. Kleiman, 454–88. Special Publication no. 7. Lawrence, Kans.: American Society of Mammalogists.

———. 1986. Ecology and social evolution in the mongooses. I *Ecological aspects of social evolution,* eds. D. I. Rubenstein and R. W. Wrangham, 131–52. Princeton, N.J.: Princeton University Press.

———. 1987. Dispersal and intergroup transfer in the dwarf mongoose. In *Mammalian dispersal patterns: The effects of social structure on population genetics,* eds. B. D. Chepko-Sade and Z. T. Halpin, 85–103. Chicago: University of Chicago Press.

Rubenstein, D. I., and Wrangham, R. W. 1986. Socioecology: Origins and trends. In *Ecological aspects of social evolution,* ed. D. I. Rubenstein and R. W. Wrangham, 3–17. Princeton, N.J.: Princeton University Press.

Schaaf, C. D. 1990. Status of the drill *(Mandrillus leucophaeus)* in captivity and in the wild. *AAZPA Regional Conference Proceedings,* 414–20. Wheeling, W.Va.: American Association of Zoological Parks and Aquariums.

Schaller, G. B. 1972. *The Serengeti lion.* Chicago: University of Chicago Press.

Shields, W. M. 1987. Dispersal and mating systems: Investigating their causal connections. In *Mammalian dispersal patterns: The effects of social structure on population genetics,* ed. B. D.

Chepko-Sade and Z. T. Halpin, 3–26. Chicago: University of Chicago Press.

Smith, A. T., and Ivins, B. L. 1983. Spatial relationships and social organization in adult pikas: A facultatively monogamous mammal. *Z. Tierpsychol.* 66:289–308.

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T., eds. 1987. *Primate societies.* Chicago: University of Chicago Press.

Spinage, C. A. 1986. *The natural history of antelopes.* New York: Facts on File Publications.

Stevens, E. F. 1987. Ecological and demographic influences on social behavior, harem stability, and male reproductive success in feral horses *(Equus caballus).* Ph.D. dissertation, University of North Carolina, Chapel Hill.

———. 1990. Instability of harems of feral horses in relation to season and presence of subordinate stallions. *Behaviour* 112 (3–4): 149–61.

Struhsaker, T. T. 1975. *The red colobus monkey.* Chicago: University of Chicago Press.

Thornhill, R., and Alcock, J. 1983. *The evolution of insect mating systems.* Cambridge, Mass.: Harvard University Press.

Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971,* ed. B. G. Campbell, 136–79. Chicago: Aldine.

Wemmer, C., and Fleming, M. J. 1975. Management of meerkats in captivity. *Int. Zoo Yrbk.* 15:74–77.

Wilson, E. O. 1975. *Sociobiology: The new synthesis.* Cambridge, Mass.: Harvard University Press.

Wittenberger, J. F. 1981. *Animal social behavior.* Boston: Duxbury Press.

Wittenberger, J. F., and Tilson, R. L. 1980. The evolution of monogamy: Hypotheses and evidence. *Annu. Rev. Ecol. Syst.* 11: 197–232.

Wolfe, J. O. 1986. Infanticide in white-footed mice, *Peromyscus leucopus. Anim. Behav.* 34:568.

Wrangham, R. W., and Rubenstein, D. I. 1986. Social evolution in birds and mammals. In *Ecological aspects of social evolution,* ed. D. I. Rubenstein and R. W. Wrangham, 452–70. Princeton, N.J.: Princeton University Press.

34

Behavioral Development and Play

KATERINA V. THOMPSON

Young mammals undergo profound physical and behavioral transformations between birth and the attainment of sexual maturity, changing from infants highly dependent on their mothers for nourishment and protection to independently functioning adults capable of dispersal or integration into the social group. During this period of maternal dependence, young mammals are buffered from the demands of the adult world, and have the opportunity for protected growth and learning. These early experiences may greatly influence adult behavior and reproductive success. Current investigations of behavioral development clearly show that immature mammals, rather than being passive recipients of experiences that modify adult behavior, are active participants in the developmental process. Young mammals display an impressive array of behavioral strategies that appear to ensure their survival and maximize their success throughout all stages of development (Bekoff 1985; Galef 1981).

Mammalian behavioral development is typically subdivided into three major periods based on the degree of maternal dependence and physical maturity (Jolly 1972). Infancy encompasses the interval from birth until weaning, and represents the period of maximal dependence on the mother. Following weaning, young animals are termed juveniles. While nutritionally independent, juveniles are frequently still dependent on their mothers (or other members of the social group) for protection from predators, physical elements, and aggressive conspecifics. The final stage of development is adulthood, the period following the attainment of sexual maturity. During the transition from the juvenile period to adulthood, animals are termed subadults. This review focuses primarily on the behavior of infant and juvenile mammals, including the general course of behavioral development in mammals as well as specific strategies adapted to various social and ecological environments.

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THE PERIOD OF DEPENDENCE

Degree of Development at Birth

Mammals vary in the extent of their physical maturation at birth, ranging from extremely undeveloped, or altricial, to well-developed, or precocial. The attributes that characterize altricial and precocial young are listed in table 34.1. The extremes of altriciality and precociality are, of course, endpoints of a continuum, and the majority of mammalian species show intermediate degrees of development (see also Kirkwood and Mace, chap. 43, this volume). Altricial young are produced by marsupials, insectivores, many rodents, rabbits, and several carnivore families, including bears, giant pandas, *Ailuropoda melanoleuca,* and weasels. Precocial young are produced by ungulates, whales, hares, and hystricomorph rodents. The young of most primate and carnivore species are intermediate, and are referred to as semialtricial or semiprecocial, depending on which traits predominate.

Some groups of mammals exhibit deviations from this basic pattern. Monotremes do not give birth to live young, but rather lay eggs. The young, when hatched, are altricial (Nowak and Paradiso 1983; Griffiths 1968). Marsupials have an extremely short gestation period and give birth to tiny young that are little more than embryos. Although rudimentary in most respects, newborn marsupials possess remarkably well developed forelimbs that are capable of grasping the mother's fur. These uniquely structured limbs allow the neonate to make its way, unassisted, from the mother's reproductive tract to her pouch or teats, where it attaches to a nipple (Ewer 1968).

Early Development of Altricial Mammals

In placental mammals, early development of altricial infants primarily involves maturation of the sensory systems and development of motor coordination (Ferron 1981; Happold 1976; Rosenblatt 1976), and has been studied extensively in domestic species such as rats, *Rattus norvegicus,* dogs,

TABLE 34.1. Characteristics of Altricial and Precocial Infant Mammals

Altricial	Precocial
Hairless or sparsely furred	Fully furred
Sensory systems undeveloped, eyes and ears closed	Functional sensory systems
Incapable of coordinated locomotion	Capable of coordinated locomotion
Unable to maintain a stable body temperature independently	Able to thermoregulate
Complete nutritional dependence on mother	Able to eat some solid food shortly after birth
Examples	Examples
Spectacled bear, *Tremarctos ornatus*	Brindled wildebeest, *Connochaetes taurinus*
Red kangaroo, *Macropus rufus*	Common zebra, *Equus burchellii*
Oriental small-clawed otter, *Amblonyx cinereus*	Patagonian cavy, *Dolichotis patagonum*

Canis familiaris, and cats, *Felis catus.* The infant's most critical tasks at this stage are initiating and sustaining sucking and maintaining contact with nestmates. Rosenblatt (1976) has surveyed the vast body of literature on early behavioral development in altricial mammals, and much of this discussion follows his review.

At birth, altricial infants are most sensitive to thermal and tactile stimuli, which are used to locate teats and maintain contact with the mother and littermates. Infants respond to any temperature change or loss of contact with nestmates by vocalizing, which stimulates parental attentiveness (mice, *Mus musculus:* Ehret and Berndecker 1986; pikas, *Ochotona princeps:* Whitworth 1984; rodents: DeGhett 1978), and by crawling in circles, which often enables them to locate nestmates. Heightened sensitivity to olfactory cues develops within days of birth, and the infants' responses to various situations become more specific. At this stage, infant rats learn to recognize the odor of their mother (Leon 1975), littermates (Hepper 1983), and the nest site (Carr, Marasco, and Landauer 1979).

The final stage of early development begins when the eyes open. This event typically coincides with hair growth and the ability to regulate body temperature. The infants then assume an active role in initiating suckling, since they can detect the mother at a distance and approach her to nurse (Walters and Parke 1965). Vision permits greatly increased mobility, exploration, and interaction with littermates. During this period infants become better coordinated and expand their behavioral repertoire. At this point, altricial infants have reached a state of maturity comparable to that of precocial mammals at birth.

Comparative studies have indicated that the timing of the development of motor skills and sensory systems is closely associated with the demands of the environment. Ferron (1981) investigated the rates of development in four species of squirrels and found that emergence from the nest was delayed in structurally complex habitats that required well-developed locomotor skills. Red squirrels, *Tamiasciurus hudsonicus,* which inhabit complex arboreal environments, showed slower physical and behavioral development than Columbian, *Spermophilus columbianus,* and golden-mantled ground squirrels, *S. lateralis,* which inhabit relatively simple terrestrial environments. Northern flying squirrels, *Glaucomys sabrinus,* had the most complex locomotor requirements and were the slowest-developing species.

Developmental landmarks for more than 400 mammalian species are tabulated in Brainard (1985) and Eisenberg (1981).

Proximity to Caregivers

Species differ in the spatial relationships that mothers and other caregivers maintain with the young. Some species maintain constant close contact with their offspring, while others leave offspring unattended for extended periods of time. Four basic groups of species can be identified: nesters, hiders, carriers, and followers.

Nesting species leave their young in a protected den or nest, returning at intervals to feed and care for them. For example, snow leopards, *Uncia uncia,* give birth to their young in rocky, fur-lined dens; the litter remains there for the first 3 months of life (Hemmer 1972). Pikas also isolate their litters in a nest, which the mother visits twice an hour for only a few minutes (Whitworth 1984).

Hiding is the predominant infant behavioral strategy among ungulates (Estes 1976). Like nesting, hiding involves intermittent mother-offspring contact, but differs from the behavior observed in nesting species in that the hiding site is chosen by the infant (Leuthold 1977; Lent 1974) rather than being prepared by the mother. It is not uncommon for hiders to choose a fresh hiding site after each bout of activity. For example, infant Kirk's dik-diks, *Madoqua kirkii,* remain in hiding for most of their first 10 to 20 days of life, lying nearly motionless in clumps of vegetation. Calves emerge from their hiding sites for brief periods to nurse in the early morning, at dusk, and during the night (Bowker 1977).

Species in the carrier group maintain constant physical contact with their infants during early development. Most primate species adopt the carrier strategy, with infants typically clinging to the fur of the mother's back, or in some species, the belly. In marmosets and tamarins, other family members assist in carrying (Mendoza and Mason 1986; Hoage 1977; Box 1975). Marsupial infants remain constantly attached to one of the mother's nipples during the first weeks or months following birth (Nowak and Paradiso 1983; Ewer 1968). The teat swells inside the infant's mouth to provide a firm attachment. In pouched marsupials, older young continue to ride in the pouch after they become mature enough to detach from the nipple, while in pouchless species, they cling to the mother's back. Other species that carry their young include sloths, giant anteaters, *Myrmecophaga tridactyla,* and some bats.

TABLE 34.2. Developmental, Ecological, and Social Correlates of Nesting, Hiding, Carrying, and Following Behavioral Strategies

	Nesting	Hiding	Carrying	Following	References[a]
Degree of development at birth	Altricial	Precocial	Semiprecocial (e.g., primates) or highly altricial (e.g., marsupials)	Extremely precocial	1, 2, 3
Body size	Usually small, occasionally large	Small relative to followers	No obvious trend	Large	2, 4
Habitat	Terrestrial or arboreal	Terrestrial	Arboreal, flying, or terrestrial	Terrestrial or aquatic	1, 5
Availability of nesting or hiding sites	Present	Present	Absent	Absent	2, 6
Home range stability	Stable	Stable	Stable or nomadic	Nomadic	4
Litter size	Large	Usually one young	Usually one or two	Usually one	1, 7

[a] 1, Ewer 1968; 2, Lent 1974; 3, Nowak and Paradiso 1983; 4, Lundrigan, unpub.; 5, Jolly 1972; 6, Estes 1976; 7, Rosenblatt 1976.

In follower species, infants accompany their mothers throughout their daily activities. This strategy is exhibited by several ungulate species (Leuthold 1977; Lent 1974; Walther 1965) and many aquatic mammals (Ewer 1968). The wildebeest, *Connochaetes taurinus*, a typical follower, displays the ability to follow its mother as soon as it can walk, often within minutes of birth (Estes and Estes 1979). In captive Nile hippopotamuses, *Hippopotamus amphibius*, infants spend virtually 100% of their time within one body length of their mothers for the first several weeks of life (Ralls, Lundrigan, and Kranz 1987a).

Nesting, hiding, carrying, and following can be interpreted as strategies for protecting vulnerable newborns from predators and accidents. The specific strategy used depends on a variety of ecological and social factors, as well as the degree of precociality of the infant (table 34.2). Most species adopt one strategy, but some species show a mixture of strategies, or show different strategies during different periods of development. For example, in several marsupials, young remain in the pouch and are carried throughout early development. Once they have outgrown the pouch, they are left alone in a nest while the mother forages (Ewer 1968; Beach 1939). Several prosimians that carry their young most of the time display a combined strategy incorporating a behavior pattern similar to hiding. This strategy, known as "parking," involves leaving the infant clinging to a tree branch unattended while the mother forages (Pereira, Klepper, and Simons 1987; Charles-Dominique 1977; Lekagul and McNeely 1977).

The strategies also differ in the relative responsibility of mother and infant for regulating proximity. In nesting species, the timing and duration of contact periods are largely determined by the mother (pikas: Whitworth 1984; rodents: Priestnall 1983). In hider species, mothers determine the timing of contact periods, but the infants take the active role in determining the duration of reunion periods by wandering away from their mothers and searching for hiding sites (Ralls, Lundrigan, and Kranz 1987b; Lent 1974). Constant proximity in carriers is maintained largely by the infants, which cling to their mothers' fur (African yellow-winged bat, *Lavia frons:* Vaughan and Vaughan 1987; primates: Jolly 1972). If infants become detached before they have gained motor coordination, however, they are dependent on their mothers to retrieve them (dusky titi monkey, *Callicebus moloch:* Mendoza and Mason 1986). Infant followers assume responsibility for maintaining contact with their mothers (harbor seals, *Phoca vitulina*: Renouf and Diemand 1984; ungulates: Lent 1974), but the mothers often encourage following by vocalizing or by postural signals such as tail wagging and head bobbing (Lent 1974).

The behavioral strategy adopted by a species largely determines the daily pattern of activity shown by infants. Since infants are highly vulnerable to predation, most activity occurs under the protective watch of adults. In species that have only intermittent contact, infants may show brief bursts of concentrated activity during periods when mother and offspring are reunited. The frequency of maternal contact also affects the distribution of nursing opportunities for the infant. The constant maternal contact provided by carrier and follower strategies allows greater flexibility and often results in more frequent suckling opportunities. Mouflon, *Ovis musimon,* which are followers, are reported to nurse every 10–15 minutes during early infancy (Pfeffer 1967). Similarly, infant chimpanzees, *Pan troglodytes,* which are carried, have been observed to nurse an average of 2.7 times per hour during the first month of life (Clark 1977). In contrast, hiding and nesting species can suck only during mother-offspring reunion periods, which may be brief and infrequent. Leuthold (1977) reviewed the early development of fourteen species of hider ungulates and noted that most had two to five sucking bouts per day. The most extreme pattern is shown by the tree shrews, nesting species in which the mother approaches the nest site only once every 48 hours to nurse the young (Martin 1968; Lekagul and McNeely 1977).

These behavioral differences appear to be associated with differences in lactation physiology. Species that nurse their young at infrequent intervals tend to produce milk that contains high concentrations of fat and the protein casein; species that nurse their young very frequently produce more dilute milk (Oftedal 1980). The pattern of maternal contact exhibited by a species thus provides clues to appropriate nonmaternal milk substitutes for infants that must be hand-reared.

Familiarity with a particular species' pattern of early behavioral development and parent-offspring proximity is essential to its successful management in captivity. Such familiarity allows the detection of deviations from the normal developmental pattern that may indicate problems. Followers that do not remain close to their mothers, carrier infants that are found separated from their parents, and nester adults that constantly carry young are all cause for concern. Knowledge of a species' early developmental history allows exhibit designers to provide the necessary environmental features so that normal developmental behaviors can be expressed. For example, hider ungulates that frequently change hiding sites need to have access to multiple potential hiding areas. Similarly, nesting species should be provided with a selection of appropriate nesting sites. Tree shrews, *Tupaia belangeri,* are among the many species that require multiple nesting sites. Females rest separately from their young, and if provided with fewer than two nest boxes, often kill their offspring (Martin 1968). Knowledge of interspecific differences in early development allows informed management decisions when temporary separation of mother and young becomes necessary for medical treatment, neonatal workups, or marking of the infant. In species with intermittent contact, the normal periods of mother-infant separation are an ideal time to gain access to the infants with a minimum of trauma. Separating infants from their mothers in constant contact species is necessarily more traumatic and disruptive.

Sucking

Sucking is a universal characteristic of mammals (Vaughan 1978), and all infant mammals are initially dependent on their mothers for nutritional support. Infants take an active role in the initiation and maintenance of sucking. Characteristic odors of the mother's teat area (rabbits, *Oryctolagus cuniculus:* Hudson and Distel 1985; rats: Teicher and Blass 1977, 1976; cats: Kovach and Kling 1967), as well as its warmth (domestic sheep: Billing and Vince 1987a, 1987b) and texture (Billing and Vince 1987a, 1987b; rabbits: Hudson and Distel 1985; cats: Rosenblatt 1971), are the primary cues used by infants to locate nipples. While sucking, infant mammals use a variety of tactics to stimulate milk delivery (reviewed by Ewer 1968, 1973). For example, infants of many species exhibit kneading, massaging of the mammary gland with their forepaws, while infant ungulates commonly engage in bunting, a forceful butting of the udder. Even in highly altricial species such as rats, infants can control the amount of milk received by modulating the vigor with which they suck (Hall and Williams 1983).

In several species, each infant within a litter sucks from a particular teat and maintains this preference throughout development. This phenomenon, known as a teat order, has been described for a wide variety of exotic animals, including African civets, *Civettictis civetta* (Ewer and Wemmer 1974), binturongs, *Arctictis binturong* (Schoknecht 1984), mountain lions, *Felis concolor* (Pfeifer 1980), snow leopards (McVittie 1978), and green acouchis, *Myoprocta acouchy* (Kleiman 1972). The function of teat orders is unknown; however, it has been suggested that they may minimize potentially harmful competition among littermates for teats (Ewer 1959, 1968). Intense sibling competition for teats was indeed observed in captive binturongs (Schoknecht 1984) and resulted in physical injuries to the cubs. In order to prevent further injury, the cubs' nails were periodically trimmed.

THE DEVELOPMENT OF INDEPENDENCE

Increasing maturity of the infant brings about changes in the quality of the mother-young relationship and a general trend toward decreased proximity. In species in which constant proximity was the rule early in development, the infant begins to wander farther away from its mother, and the mother's attempts to limit the infant's forays decrease (ungulates: Ralls, Lundrigan, and Kranz 1987a; domestic horses: Crowell-Davis 1986; cotton-top tamarins, *Saguinus o. oedipus:* Cleveland and Snowdon 1984; baboons, *Papio anubis:* Nash 1978; yellow baboons, *Papio cynocephalus:* Altmann 1978; rhesus macaques, *Macaca mulatta:* Hinde and Spencer-Booth 1967). Infants of species with intermittent contact show an increased tendency to be active in the absence of the mother (white-tailed deer, *Odocoileus virginianus:* Nelson and Woolf 1987; pika: Whitworth 1984; roe deer, *Capreolus capreolus:* Espmark 1969). In both primates (Hauser and Fairbanks 1988; Altmann 1978; Nash 1978; Hinde 1977) and ungulates (Lickliter 1984; Espmark 1969) there is a gradual shift toward greater responsibility on the part of the infant for maintaining proximity.

Sex Differences in the Development of Independence

Male and female mammals typically differ in their adult social roles. In such species, sex differences in behavior often have their roots in the earliest interactions of mother and infant. These species typically show a matrilineal social organization: females remain throughout their lives in the groups in which they were born, while males emigrate at sexual maturity (Melnick and Pearl 1987). Table 34.3 summarizes sex differences in early development in social cercopithecine primates, in which this phenomenon has been most thoroughly documented. The trend is for mothers to behave in ways that promote early independence in their sons. In contrast, immature females engage in frequent and prolonged interactions with their mothers, other adult females, and younger infants. Social grooming among primates is often interpreted as a mechanism for building and strengthening bonds between group members (Dunbar 1980, 1984; Seyfarth and Cheney 1984; Seyfarth 1977); thus these frequent grooming bouts between immature female primates and other female group members may form the matrix upon which the social group is built and maintained.

Parent-Offspring Conflict

Conflict between mother and offspring during this period of growing independence is a normal and expected feature of behavioral development. This conflict arises because an offspring shares only half of its genes with each parent, and therefore its interests cannot be expected to coincide completely with those of its parents (Trivers 1974). Clashes between parent and offspring arise over the amount and du-

TABLE 34.3. Sex Differences in Behavioral Development of Selected Cercopithecine Primates

Sex difference	Species	References
Female infants spend more time in contact with their mothers than do male infants	Rhesus macaque, *Macaca mulatta*	White and Hinde 1975
	Pigtail macaque, *Macaca nemestrina*	Jensen, Bobbitt, and Gordon 1968
	Kra macaque, *Macaca fascicularis*	Thommen 1982
	Vervet monkey, *Chlorocebus aethiops*	Fairbanks and McGuire 1985
	Patas monkey, *Erythrocebus patas*	Loy and Loy 1987
Male infants assume a greater role in maintaining proximity with their mothers	Rhesus macaque, *Macaca mulatta*	Berman 1984
	Japanese macaque, *Macaca fuscata*	Glick et al. 1986
Mothers reject nursing attempts of sons more than those of daughters	Rhesus macaque, *Macaca mulatta*	Berman 1984; White and Hinde 1975
	Kra macaque, *Macaca fascicularis*	Thommen 1982
	Pigtail macaque, *Macaca nemestrina*	Jensen, Bobbitt, and Gordon 1968
Grooming interactions are more frequent between mothers and daughters than between mothers and sons	Patas monkey, *Erythrocebus patas*	Loy and Loy 1987
	Vervet monkey, *Chlorocebus aethiops*	Fairbanks and McGuire 1985
Grooming interactions are more frequent between female infants and unrelated adult female group members	Patas monkey, *Erythrocebus patas*	Loy and Loy 1987
Female immatures are more likely to behave maternally toward infants	Patas monkey, *Erythrocebus patas*	Loy and Loy 1987
	Olive baboon, *Papio anubis*	Hendy 1986
	Yellow baboon, *Papio cynocephalus*	Hendy 1986
	Chacma baboon, *Papio ursinus*	Cheney 1978; Seyfarth, Cheney, and Hinde 1978

ration of parental care, with parents attempting to limit the total care provided to any particular offspring so that they are better able to care for other offspring.

Conflict may be manifested in virtually all aspects of the mother-offspring relationship, including maintenance of proximity (yellow baboons: Altmann 1978), parental comforting of distressed infants (vervet monkeys, *Chlorocebus (=Cercopithecus) aethiops:* Hauser 1986), and access to the maternal pouch in marsupials (Ewer 1968). The most widely reported manifestation of parent-offspring conflict involves disputes over suckling and is often termed weaning conflict. Infants predictably "disagree" with their mothers about the duration and frequency of individual nursing bouts and the age at which weaning occurs.

As the infant grows, its demands for care tend to increase; however, its increasing self-sufficiency allows the parent to limit the amount of care provided. Therefore, the intensity of parent-offspring conflict tends to increase with time (Trivers 1974). The proportion of the infant's attempts to initiate suckling that are successful decreases as the infant ages in many species (cervids: Gauthier and Barrette 1985; vervet monkeys: Lee 1984; pika: Whitworth 1984; bighorn sheep, *Ovis canadensis:* Berger 1979b; chimpanzees: Clark 1977). Occasionally, this decrease in sucking success is accompanied by increased maternal aggression toward her offspring (pikas: Whitworth 1984; bighorn sheep: Berger 1979b; baboons: Nash 1978). Furthermore, as the infant ages, those sucking bouts that are successful are more likely to be terminated by the mother than by the infant (cervids: Espmark 1969; Gauthier and Barrette 1985; harbor seals: Renouf and Diemand 1984), suggesting that the infant is not being permitted to drink to satiety (Berger 1979b).

Parker and McNair (1979) predicted that infants should thwart their parents' attempts to limit care by exaggerating their need. Sable antelope calves, *Hippotragus niger,* for example, display a multitude of behavioral tactics apparently aimed at increasing sucking opportunities (pers. obs.). In early infancy, the calf grasps the teats directly to initiate sucking and nurses silently. As the mother begins to resist sucking attempts and terminates sucking bouts before the calf is satiated, the calf's strategy changes. Prior to grasping a teat, the calf may spend several seconds nuzzling its mother's side until she remains still and permits sucking. If the mother attempts to walk away, the calf moves in front of her to impede her forward motion, then resumes nuzzling her. During successful sucking bouts, the infant makes a high-pitched, whimpering vocalization. If the bout is terminated by the mother, the infant continues to vocalize and makes repeated attempts to reinitiate sucking. Young commonly revert to infantile behavior, implying helplessness, in order to gain additional parental care (Trivers 1985), and this may be the reason for the sable calf's whimpering vocalizations.

More extreme tactics are occasionally employed. Clark (1977) and Van Lawick-Goodall (1968) describe temper tantrums by infant chimpanzees whose sucking attempts were rebuffed. Trivers (1985) interprets such tantrums as a form of psychological manipulation, a threat by the infant to harm itself if the parent refuses to accede to its demands.

Weaning and the Transition to Adult Feeding

The transition to adult feeding is perhaps the most critical milestone in early mammalian development. In some species, weaning is abrupt and highly predictable. For example, hooded seal pups, *Cystophora cristata,* which show the shortest period of sucking known among mammals, are completely weaned at 3–5 days of age (Bowen, Oftedal, and Boness 1985). For the vast majority of species, however, weaning is a slow, gradual process characterized by decreasing milk intake and a corresponding increase in the consumption of solid food (African elephants, *Loxodonta africana:* Lee and Moss 1986; cervids: Gauthier and Barrette 1985; baboons: Rhine et al. 1985; Nash 1978).

Weaning is ultimately achieved through the efforts of both mother and young. Mothers may discourage sucking by adopting postures that make it difficult for the young to reach the nipples (tree shrews: Martin 1968), and often actively reject sucking attempts (vervet monkeys: Hauser and Fairbanks 1988; cervids: Gauthier and Barrette 1985; cotton-top tamarins: Cleveland and Snowdon 1984; baboons: Nash 1978). Additionally, mothers may promote independent feeding by bringing food items to the young (beavers, *Castor canadensis:* Patenaude 1983; golden lion tamarins, *Leontopithecus rosalia:* Hoage 1982; dholes, *Cuon alpinus:* Johnsingh 1982; cats: Leyhausen 1979). Young of some species contribute to the weaning process by decreasing their attempts to suck as they grow increasingly able to provide for themselves (Roberts, Thompson, and Cranford 1988). Maturing juveniles apparently reach a stage at which the mother's milk cannot supply enough energy to maintain their growth, and thus independently switch to alternative food sources (Galef 1981).

Most infants are capable of adequately feeding themselves long before the complete cessation of sucking. African elephant calves, for example, normally suck for about 5 years, but calves orphaned at only 2 years of age can survive on solid food alone (Lee and Moss 1986). Additionally, the timing of weaning appears to be sensitive to the availability of solid food in the environment (vervet monkeys: Lee 1984; bighorn sheep: Berger 1979b). In captivity, where food is plentiful, weaning may occur weeks or even months earlier than in free-ranging populations (Ewer 1973). For example, free-ranging musk oxen, *Ovibos moschatus,* may continue nursing for a year or more after birth (Tener 1965), but a hand-reared individual weaned itself at only 139 days of age (Banks 1978). Thus, the time at which infants first become nutritionally independent is difficult to pinpoint using behavioral indicators and often can be determined only through anecdotes or experimental means.

Making the transition from nursing to eating solid food is far more complex than simply substituting one type of food for another. The process can involve engaging in specialized behaviors that prepare the infant's digestive system for the digestion of solid food, learning to discriminate appropriate foods from potentially harmful ones, and developing complex food acquisition skills, such as hunting (see also Fernandes, chap. 35, this volume).

In herbivores, digestion of plant material depends on microorganisms living in the animal's gut. At birth, the digestive system is virtually devoid of these essential microorganisms (Eadie and Mann 1970), and young must inoculate themselves to enable their digestive systems to assimilate plant material. Behaviors that may serve this purpose include licking the lips and tongue of the mother, which could result in the transfer of microbes in the saliva (Hungate 1968), feeding on plants that have maternal saliva remaining on them (elephants: Eltringham 1982), and eating the feces of the mother or other adults (domestic horses, *Equus caballus:* Crowell-Davis and Houpt 1985; African elephants: Guy 1977). Koalas, *Phascolarctos cinereus,* have a specialized method for transferring digestive microbes from mother to offspring. At about 5 months of age, when the infant's teeth are beginning to erupt, the mother begins producing special fecal matter composed of partially digested plant matter from the cecum, the organ in which microbial digestion occurs. The infant koala receives feedings of this material at 2- to 3-day intervals for 1–6 weeks, after which it is capable of feeding independently (Thompson 1986; Martin and Lee 1984).

Preferences for particular food items may be acquired through observation and imitation of the mother (Provenzo and Balph 1987; Leuthold 1977). Moose calves, *Alces alces,* for example, develop food preferences by first feeding simultaneously with their mothers on a single plant. Later in development, calves feed on separate plants of the same species that their mother is eating before making the final transition to selecting forage independently (Edwards 1976). In species in which adults provision the young, preferences may be learned through food sharing. At 4–5 weeks of age, golden lion tamarins regularly touch, sniff, and taste food items being consumed by their carriers (Hoage 1982). Soon after this period of investigation, the infants begin to snatch food away from family members and consume it. Preferences for certain types of solid food may be well developed long before weaning occurs at 11–15 weeks.

Learning may play an even greater role in the development of adult feeding in carnivores. The domestic cat, a solitary hunter, learns hunting skills through maternal encouragement and supervision (Leyhausen 1979). Early in development, mother cats bring prey back to the den and allow their kittens to observe its consumption. Soon after, dead prey, and later live prey, is provided for the kittens to manipulate and eat. Prey that manage to evade the kittens are recaptured by the mother and returned to the kittens. After several weeks of exposure and practice, the kittens develop sufficient hunting skills to dispatch prey independently.

Cooperative hunters, such as the social canids, show a similar dependence on learning. Dhole pups are first given regurgitated food by adults. Later, the pups are brought to the sites of kills to feed. Shortly after weaning, the pups accompany the pack on hunts, but it may be several months before the pups actually assist in making a kill (Johnsingh 1982).

Parents, particularly the mother, often play prominent roles in the acquisition of feeding skills, and premature separation of infants from their family groups may have lasting detrimental effects. Even young that are no longer nursing may be dependent on their parents for acquiring food preferences and honing feeding skills critical to their future survival and well-being. Van Lawick-Goodall (1971) reported that a 5-year-old chimpanzee juvenile, orphaned 2 years before, showed deficits in termite foraging compared with his peers, suggesting that this important feeding skill is in part developed through mother-offspring interaction.

Premature separation of mother and infant may also result in aberrant feeding behaviors. Regurgitation and reingestion of food is widespread among captive gorillas, *Gorilla gorilla,* yet absent in the wild. Wild-caught and captive-born hand-reared gorillas show much higher rates of regurgitation and reingestion than captive-born mother-reared individuals, leading Gould and Bres (1986) to speculate that this abnormal behavior results from deficits in early social development.

Predatory species in particular may be permanently affected by a lack of experience with prey items in early development. Domestic kittens separated from their mothers at an early age and with no prior exposure to live prey often show a lack of ability or inclination to hunt live prey in adulthood (Ewer 1973; Leyhausen 1965). Similarly, there are anecdotes illustrating the extreme difficulty of encouraging normal hunting behavior in captive big cats returned to the wild (Adamson 1969, 1960). The obstacles faced by Adamson's lion, *Panthera leo,* and cheetah, *Acinonyx jubatus,* could be attributed to their having passed the age at which hunting skills were most easily learned (Ewer 1973).

Interaction with conspecifics is as important in captive populations as in free-ranging ones, since such interaction may allow the learning of feeding skills specific to the captive environment. If captive-born young must be hand-reared, prompt reintroduction to adult conspecifics may allow the development of normal feeding strategies. Providing a captive environment that allows the normal development of feeding skills is critically important when reintroduction to the wild is a goal. Animals deprived of early experience may never become fully competent at foraging in a natural setting.

PLAY

As the infant becomes less dependent on its mother, it begins to interact more frequently with littermates, peers, and other members of the social group. Among the most conspicuous social activities exhibited by young mammals at this stage is play. In addition to social play, two other forms of play that may sometimes occur in a social context are locomotor play and object play.

Play is nearly ubiquitous among mammals. In his comprehensive review of the natural history of animal play behavior, Fagen (1981) found descriptions of juvenile play in all mammalian orders except the relatively poorly studied flying lemurs (order Dermoptera), aardvarks (order Tubulidentata), and hyraxes (order Hyracoidea). Play appears to be especially frequent and elaborate in the primates, carnivores, ungulates, and rodents, and it is in these taxonomic groups that play has been most thoroughly studied.

Types of Play

Play is commonly subdivided into three basic categories: object, locomotor, and social (Fagen 1981). These categories are not entirely mutually exclusive, however, since object and locomotor play frequently occur in social contexts, and elements of all three types of play frequently occur within single play bouts.

Object play involves repetitive manipulation of things in the infant's environment, and can be quite remarkable in its diversity. Goodall (1986) listed sticks, stones, dry dung, small fruits, fruit-laden twigs, and strips of skin and hair from old kills as among the favored play objects of juvenile chimpanzees. These objects were carried, thrown on the ground, used for self-tickling, rubbed on the body, rolled on the ground, thrown hand to hand, and thrown in the air to be caught or retrieved.

Object play often incorporates behaviors used in foraging or in the handling and capture of live prey, although many of the more inventive manipulations have no obvious parallel in the adult behavioral repertoire. It may occur in social as well as solitary contexts, for example, when two or more infants vie for possession of an object. Additionally, the focus of object play may itself be another animal, as when a young predator toys with a live prey item, or a juvenile playfully manipulates the body parts of its parents.

Locomotor play is composed of vigorous body movements such as running, jumping, head tossing, and body twists (Wilson and Kleiman 1974). More spectacular locomotor behaviors, such as back flips performed by rhesus macaques (Symons 1978), whirling around in the air by mountain goat kids, *Oreamnos americanus* (Dane 1977), and breaching and surf riding by infant whales (Fagen 1981), vary with the species' morphology and ecology. In general, locomotor play bears a strong resemblance to the behaviors seen in predator evasion.

Social play differs from other types of play in that it is truly interactive. It involves two or more individuals, each of whose movements are oriented toward the other and whose responses are influenced by the other's actions. Common forms of social play include play fighting, which mimics serious fighting, and approach-withdrawal play, in which individuals take turns chasing and being chased. Social play may also include elements of reproductive behavior, such as mounting.

Ontogeny of Play Behavior

Play begins early in postnatal ontogeny, shortly after infants have developed locomotor skills adequate to perform playful movements (Fagen 1976). Primates are a notable exception to this trend, with several species showing playful manipulation of objects well before they are capable of coordinated locomotion. In general, solitary forms of play (object and locomotor play) precede social forms in ontogeny (squirrel monkeys, *Saimiri sciureus:* Baldwin 1969; Nilgiri langurs, *Trachypithecus (=Presbytis) johnii:* Poirier 1968, 1970; cats: West 1974; Cuvier's gazelle, *Gazella cuvieri:* Gomendio 1988).

There is a general trend toward increasing play complexity and more interactive play as the infant matures (Baldwin 1986). For example, in domestic cats, play first appears at 4 weeks of age in the form of single play behavior patterns performed in solitary contexts. Soon after, kittens begin to create sequences of play behaviors by stringing together several repetitions of a single behavior pattern. At 5 weeks of age, these behavior patterns begin to appear in social contexts, directed at other kittens, and play bouts often involve sequences of two or three different play behaviors. Finally, during the 6th week, kittens are able to perform complex sequences containing as many as eight different play behavior patterns (West 1974).

Although play frequency, complexity, and duration peak during infancy and the juvenile period, play often persists into adulthood. The vast majority of adult play is social play with infants and juveniles. In free-ranging rhesus macaques, for example, 75% of adult play bouts involved immature individuals younger than 3 years of age, while only 25% of bouts involved two adults (Breuggeman 1978). Adults typi-

Table 34.4. Characteristics Distinguishing Social Play from Aggression in the American Black Bear, *Ursus americanus*

Features distinguishing play	Examples
Some agonistic behaviors are never exhibited during play.	Components of agonistic behavior that are absent from juvenile social play include jaw snapping, swatting the ground, aggressive vocalizations, and erection of the fur on the neck and back.
Some behaviors are exhibited exclusively in the context of play.	Components of juvenile social play that are absent from agonistic interactions include head butting, muzzle seizing, hind-leg clawing, and nipping.
Some behaviors may be performed with greater frequency in play.	Biting, licking, biting intention movements, and swiping with the pad of the foot are exhibited significantly more frequently in juvenile social play than in agonistic interactions of similar duration.
Play may be less predictable and more variable.	Biting, clawing, and mounting are more variable in orientation and directed at more target areas in social play than in agonism.
Behaviors from different contexts may be interspersed during single play bouts.	Mounting, a component of adult sexual behavior, is incorporated into sequences of juvenile social play almost ten times as frequently as it appears during adult agonistic interactions.

Source: Henry and Herrero 1974.

cally do not play indiscriminately with all immatures, but rather favor playing with their offspring and younger siblings. Feral horse stallions show a remarkable ability to discriminate between their own offspring and unrelated foals, playing with their sons six times more than with unrelated, similarly aged male foals (Berger 1986). Parent-offspring play has been reported for a wide variety of taxonomic groups, including marsupials (Croft 1981; Kaufman 1975; Herrmann 1971), primates (Breuggeman 1978; Maple and Zucker 1978; Zucker, Mitchell, and Maple 1978; Sussman 1977; Hrdy 1976; Van Lawick-Goodall 1968, 1967), rodents (Wilson and Kleiman 1974), ungulates (Fagen 1981; Espmark 1971; Mohr 1968; Walther 1962), and carnivores (Kleiman and Malcolm 1981). In species that bear singleton offspring, adults rather than peers may be the primary play partners (euros, *Macropus robustus:* Croft 1981; lemurs, *Lemur* spp.: Sussman 1977; whiptail wallabies, *Macropus parryi*: Kaufmann 1975; orangutans, *Pongo pygmaeus:* MacKinnon 1974; eastern gray kangaroo, *Macropus giganteus:* Herrmann 1971).

General Characteristics of Juvenile Play

Theorists have had great difficulty formulating a comprehensive definition of play behavior because it is so diverse and so closely resembles other types of behavior, such as aggressive combat, prey catching, and predator avoidance (Martin and Caro 1985; Fagen 1981). Martin and Caro (1985), after reviewing various definitions of play, concluded that play is best characterized by the *absence* of the endpoints in which "serious" versions of the behavior patterns culminate. For example, play fighting does not result in injury or differential access to a disputed resource; likewise, predatory play does not involve killing and consuming prey.

Several additional characteristics seem to differentiate play behavior from its serious equivalents. The sequence in which behavioral components occur may be reordered (Loizos 1966) or less predictable (canids: Bekoff 1974). Play bouts commonly incorporate behaviors usually seen in various unrelated contexts. For example, in the degu, *Octodon degus,* and the choz-choz, *Octodontomys gliroides,* two South American rodent species, elements of fighting behavior are interspersed with jumping and running, behaviors otherwise used in predator avoidance (Wilson and Kleiman 1974). Certain behaviors may be exhibited more frequently in play (American black bears, *Ursus americanus:* Henry and Herrero 1974; Loizos 1966), while others are always absent. Additionally, during play bouts, animals are more likely to alternate dominant and submissive roles than in serious fighting (squirrel monkeys: Biben 1986; baboons: Owens 1975a). Characteristics distinguishing social play from serious fighting in the American black bear are shown in table 34.4.

Possible Functions of Juvenile Play

There has been much speculation about the precise benefits young animals receive from play, but research in this area has been sparse, and the function of play remains obscure. Baldwin (1986), in his review of primate play behavior, was able to identify no fewer than thirty-two different proposed benefits of play, ranging from optimizing physiological development (Brownlee 1954) to promoting normal personality development (Harlow and Harlow 1969). Martin and Caro (1985), Fagen (1981), and Smith (1982) provide excellent reviews of the various proposed functions of play and the evidence supporting and refuting them.

Play has not lent itself to straightforward scientific investigation. The very nature of play, intermixing behavior patterns from widely divergent contexts, makes its purpose difficult to decipher. The physical appearance of play and the context in which it occurs provide few clues as to how it might improve a youngster's ability to survive or reproduce. Furthermore, researchers have found it impossible to deprive juveniles of play experimentally without simultaneously altering many other aspects of their social behavior. The behavioral deficits exhibited by animals in such play

TABLE 34.5. Play Signals Exhibited by a Representative Sample of Species

Behavior	Species	Reference
Vocalization	Squirrel monkey, *Saimiri sciureus*	Biben and Symmes 1986 Winter, Ploog, and Latta 1966
	Hamadryas baboon, *Papio hamadryas*	Leresche 1976
	Cotton-top tamarin, *Saguinus oedipus*	Goedeking 1985
	Vervet monkey, *Chlorocebus aethiops*	Struhsaker 1967
	Chimpanzee, *Pan troglodytes*	Van Lawick-Goodall 1968
	Gorilla, *Gorilla gorilla*	Schaller 1963
	Baboon, *Papio anubis*	Owens 1975b
	Degu, *Octodon degus*	Wilson 1982
	Dwarf mongoose, *Helogale parvula*	Rasa 1984
Play face	Mouse lemur, *Microcebus coquereli*	Pages 1983
	Tarsier, *Tarsius bancanus*	Niemitz 1974
	Common marmoset, *Callithrix jacchus*	Stevenson and Poole 1982
	Hamadryas baboon, *Papio hamadryas*	Leresche 1976
	Chimpanzee, *Pan troglodytes*	Hayaki 1985
	Japanese macaque, *Macaca fuscata*	Koyama 1985
	Rhesus macaque, *Macaca mulatta*	Symons 1978
	Yellow-bellied marmot, *Marmota flaviventris*	Jamieson and Armitage 1987
	Black bear, *Ursus americanus*	Henry and Herrero 1974
	African lion, *Panthera leo*	Schaller 1963
	Polecat, *Mustela putorius*	Poole 1978
	Collared peccary, *Pecari tajacu*	Byers 1985
	Tiger quoll, *Dasyurus maculatus*	Fagen 1981
	Choz choz, *Octodontomys gliroides*	Fagen 1981
Crescent or flattened ears	Black bear, *Ursus americanus*	Henry and Herrero 1974
Tail up	Reedbuck, *Redunca arundinum*	Jungius 1971
Gambol, stagger	Rhesus macaque, *Macaca mulatta*	Symons 1978
Odors	Short-tailed vole, *Microtus agrestis*	Wilson 1973

deprivation experiments cannot be attributed simply to the lack of opportunity to play (Bekoff 1976).

In his review of ungulate play, Byers (1984) evaluated the possible functions of play based on differences and similarities among species. Locomotor movements were common to all species and were the only form of play exhibited by some, leading Byers to suggest that play in ungulates, and perhaps other mammals as well, evolved to promote optimal physiological development. As competition among males for mates became more common, social play developed as practice for adult combat. Byers further suggested that in some species, such as the collared peccary, *Pecari (=Tayassu) tajacu,* play has assumed an additional function of maintaining group cohesion. Other species, experiencing different evolutionary selection pressures, may have developed different secondary functions for play behavior.

The form and content of juvenile play have undoubtedly been shaped by many factors that vary from species to species. It is probable that no single hypothesis will explain all types of play, and each function may not be of equal importance to all species. In spite of a recent surge of interest in play behavior, there is not a single species for which the function of play has been unambiguously determined.

Play Signals and Solicitation Behaviors

Play is frequently accompanied by the presence of play signals, communicatory behaviors that occur virtually exclusively in the context of play. These signals, typically vocalizations or facial expressions, may be displayed almost continuously throughout play bouts, and, because of their specificity, are useful indicators of the playful nature of social interactions.

Examples of behaviors from a variety of sensory modalities that have been identified as play signals are given in table 34.5. The play face (figure 34.1), characterized by a relaxed, open-mouthed expression with the lips usually covering the teeth, appears to be an almost universal mammalian play signal. Other play signals, such as play vocalizations, tend to be more species-specific. For example, degus "gurgle" during social play (Wilson 1982; Wilson and

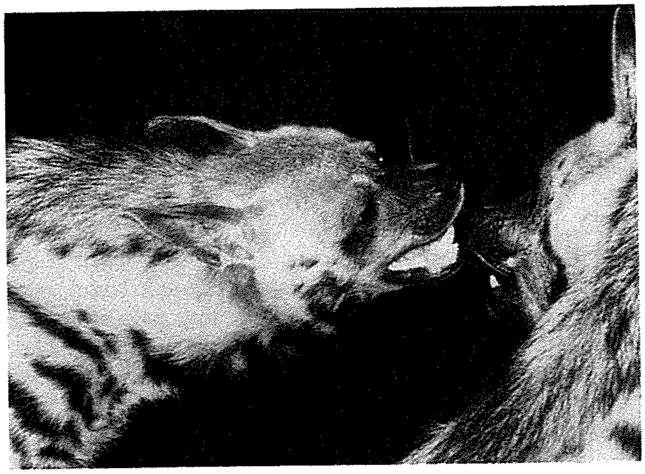

FIG. 34.1. Two striped hyenas, *Hyaena hyaena,* exhibiting play faces during a play bout. (Photo courtesy of Lee Miller.)

Kleiman 1974), while squirrel monkeys produce a high-pitched "peep" (Biben and Symmes 1986). In still other species, play is silent, and any vocalization emitted is an indication that play has become too rough and one of the participants is unwilling to continue the play bout (Fagen 1981). Olfactory play signals are probably more widespread than table 34.5 would suggest. It is likely that olfactory signals accompany visual and auditory indicators of play in species that depend heavily on chemical modes of communication.

In addition to play signals, certain specific behaviors, known as play solicitation behaviors, tend to be associated with the initiation of social play bouts. Representative play solicitation behaviors are given in table 34.6. While many patterns appear to be specific to certain taxonomic groups, others, denoted by asterisks in table 34.6, are common to a wide variety of mammalian species. Play solicitation behaviors appear to be of two major types: (1) locomotor movements such as head tossing, body rotation, rolling over, and bouncy gaits (termed locomotor-rotational movements by Wilson and Kleiman 1974), and (2) brief, sudden physical contact such as pouncing, nipping, nudging, and batting with the paws. Locomotor-rotational play movements are perhaps associated with the initiation of play bouts because they are unlikely to be confused with real aggressive communication signals. Play solicitations involving sudden physical contact may be more likely to be misinterpreted as actual aggression, and may therefore be restricted to play interactions among animals who are already familiar with each other.

Interspecific Differences in Play Content and Frequency

The form and content of juvenile play vary widely among species (fig. 34.2), and in general parallels the behavior and ecology of adults. Social play is structurally similar to adult fighting or sexual behavior (Fagen 1981). Examples of social play and serious aggression from three mammalian orders illustrate this point. In the punaré, *Thrichomys apereoides,* both aggression and play are characterized by upright sparring, in which the participants stand on their hind legs and push against each other's shoulders in an attempt to knock each other off balance (Thompson 1985). Escalated fighting in rhesus macaques consists of wrestling, grappling, and biting the opponent. Similar behaviors predominate in juvenile play, although bites are inhibited and inflict no damage (Symons 1978). In bighorn sheep, the principal components of both play and aggression are rearing and head butting (Berger 1979a).

Carnivorous species from a wide variety of taxonomic groups incorporate elements of predatory behavior into social play and play with objects. The lion, a carnivore, the tiger quoll, *Dasyurus maculatus,* a carnivorous marsupial, and the grasshopper mouse, *Onychomys leucogaster,* an insectivorous rodent, all show the predatory behavior pattern "pounce" as part of their play repertoire (Davies and Kemble 1983; Schaller 1972). Subtle differences among species in the structure of predatory play reflect differences in adult hunting strategies (Biben 1982a). The object play of the crab-eating fox, *Cerdocyon thous,* a solitary hunter, tends to be solitary in nature, with pups frequently attempting to monopolize objects and stealing them from littermates. In contrast, the play of the cooperatively hunting bush dog, *Speothos venaticus,* includes frequent bouts of noncompetitive group play with objects, in which several pups jointly carry sticks or stones. Biben (1982a) found a general trend among the carnivores for species that are solitary hunters to engage in solitary play with objects and for cooperative hunters that share food to participate more in group object play.

At the opposite end of the spectrum, play in species that are often the targets of predation is largely composed of locomotor behaviors that are prominent components of predator avoidance (reviewed by Byers 1984; Wilson and Kleiman 1974). Wilson and Kleiman (1974), in their broad comparative study of locomotor play, noted a general relationship between the level of predation risk and the frequency of locomotor play. In species in which predation risks were high, such as rodents and ungulates, locomotor play formed a significant portion of the entire play repertoire, while species having little predation pressure, such as seals, rarely exhibited locomotor play.

When differences in play frequency, as opposed to play content, among taxa are considered, the trends are less clear. Far too few quantitative studies of related species have been conducted to permit broad generalizations, and in most cases methodological differences among studies preclude direct comparisons. Even where detailed information exists, trends are ambiguous. Fagen (1981) reported a general tendency for juvenile social play frequency to be positively correlated with measures of sociality such as adult group size and adult tolerance of conspecifics. Groups that seem to show such an association include North American canids (Fox et al. 1976; Bekoff 1974), marmots (Barash 1976), and deer (Fagen 1981). This trend, however, may be simply a result of differences in the numbers of available playmates, rather than a reflection of a species' innate propensity to play (Fagen 1981). Even species that are solitary in nature, such as the orangutan, show high frequencies of play when play partners are available (Maple 1980; Zucker, Mitchell, and Maple 1978). Additionally, there are many taxonomic groups, such as the South American canids (Biben 1983), that show no relationship between play frequency and sociality. The relationship between play frequency and sociality remains obscure.

It has been suggested that aquatic species should show more frequent play than terrestrial species (Burghardt 1988, 1984). Since water is an energy-efficient medium in which to move, the vigorous motor patterns characteristic of play would require lower energy expenditures by aquatic species than by terrestrial ones. Play frequency data on comparable terrestrial and aquatic species are lacking, however. As Burghardt (1988) noted, many of the species commonly thought of as highly playful, such as the otter, *Lontra (=Lutra) canadensis,* are indeed aquatic.

Sex Differences in Play

There is a general trend among mammals for male juveniles to exhibit more social play than their female peers (Meaney, Stewart, and Beatty 1985). This trend appears to be correlated with the degree of sexual dimorphism in adult

TABLE 34.6. Representative Play Solicitation Behaviors

Species	Behavior patterns[a]	References
Primates		
Common marmoset *Callithrix jacchus*	Pounce,* bat partner with hands,* stalk, bouncy approach*	Stevenson and Poole 1982
Squirrel monkey *Saimiri sciureus*	Leap toward partner,* roll over,* swing from perch in front of partner	Biben 1986
Rhesus macaque *Macaca mulatta*	Transverse body rotation,* play bow,* crouch-stare, roll on back*	Symons 1978; Sade 1973
Japanese macaque *Macaca fuscata*	Stare*	Koyama 1985
Chimpanzee *Pan troglodytes*	Stare,* play walk, sit facing away from partner, finger wrestle	Goodall 1986; Hayaki 1985
Rodents		
Grasshopper mouse *Onychomys leucogaster*	Roll over on back*	Davies and Kemble 1983
Yellow-bellied marmot *Marmota flaviventris*	Nose push,* somersault*	Jamieson and Armitage 1987
Columbian ground squirrel *Spermophilus columbianus*	Jump,* nudge,* paw,* pounce*	Steiner 1971
Norway rat *Rattus norvegicus*	Charge, pounce*	Poole and Fish 1975, 1976
Choz choz *Octodontomys gliroides*	Head shake,* body twist*	Wilson and Kleiman 1974
Salt desert cavy *Dolichotis salinicola*	Head shake,* body twist*	Wilson and Kleiman 1974
Insectivores		
Hedgehog *Erinaceus europaeus*	Chase, rub against partner	Poduschka 1969
Carnivores		
European badger *Meles meles*	Head sway*	Eibl-Eibesfeldt 1950
Polecat *Mustela putorius*	Pounce*	Poole 1966
Domestic cat *Felis catus*	Pounce,* play bow*	Martin 1984; West 1974
Black bear *Ursus americanus*	Rear, paw,* play bite,* head butt, lunge	Henry and Herrero 1974
Crab-eating raccoon *Procyon cancrivorus*	Twist body,* hop*	Lohmer 1976
African lion *Panthera leo*	Bouncy approach,* roll on back,* play bite,* nudge,* play bow*	Schaller 1972
Wolf *Canis lupus*	Bouncy approach,* head toss,* paw at face of partner,* play bow*	Bekoff 1972, 1974
Giant panda *Ailuropoda melanoleuca*	Somersault*	Wilson and Kleiman 1974
Odd-Toed Ungulates		
Tapir *Tapirus indicus*	Push with head*	Frädrich and Thenius 1972; Richter 1966
Square-lipped rhinoceros *Ceratotherium simum*	Head toss,* prance*	Owen-Smith 1973, 1975
Asian rhinoceros *Rhinoceros unicornis*	Head toss*	Buechner et al. 1975
Even-Toed Ungulates		
Bighorn sheep *Ovis canadensis*	Neck twist,* gambol,* heel kick	Berger 1980
Reedbuck *Redunca arundinum*	Head down*	Jungius 1971
Pygmy hippopotamus *Hexaprotodon liberiensis*	Agitate water, lie on side, gape	Wilson and Kleiman 1974
Cuvier's gazelle *Gazella cuvieri*	Rotation of head and neck*	Gomendio 1988

TABLE 34.6. *Continued*

Species	Behavior patterns[a]	References
Pinnipeds		
Stellar sea lion *Eumetopias jubatus*	Head toss,* nip*	Gentry 1974; Farentinos 1971
Harbor seal *Phoca vitulina*	Head-over-back	Wilson and Kleiman 1974
Marsupials		
Kowari *Dasycercus byrnei*	Grasp partner's head or body with forepaws	Meissner and Ganslosser 1985
Whiptail wallaby *Macropus parryi*	Paw at face of partner,* grasp partner's head	Kaufmann 1974
Sirenia		
Manatee *Trichechus manatus*	Roll on back,* rub up against partner	Hartman 1979

[a] Asterisk indicates play solicitation behaviors exhibited in a wide variety of mammalian taxonomic groups.

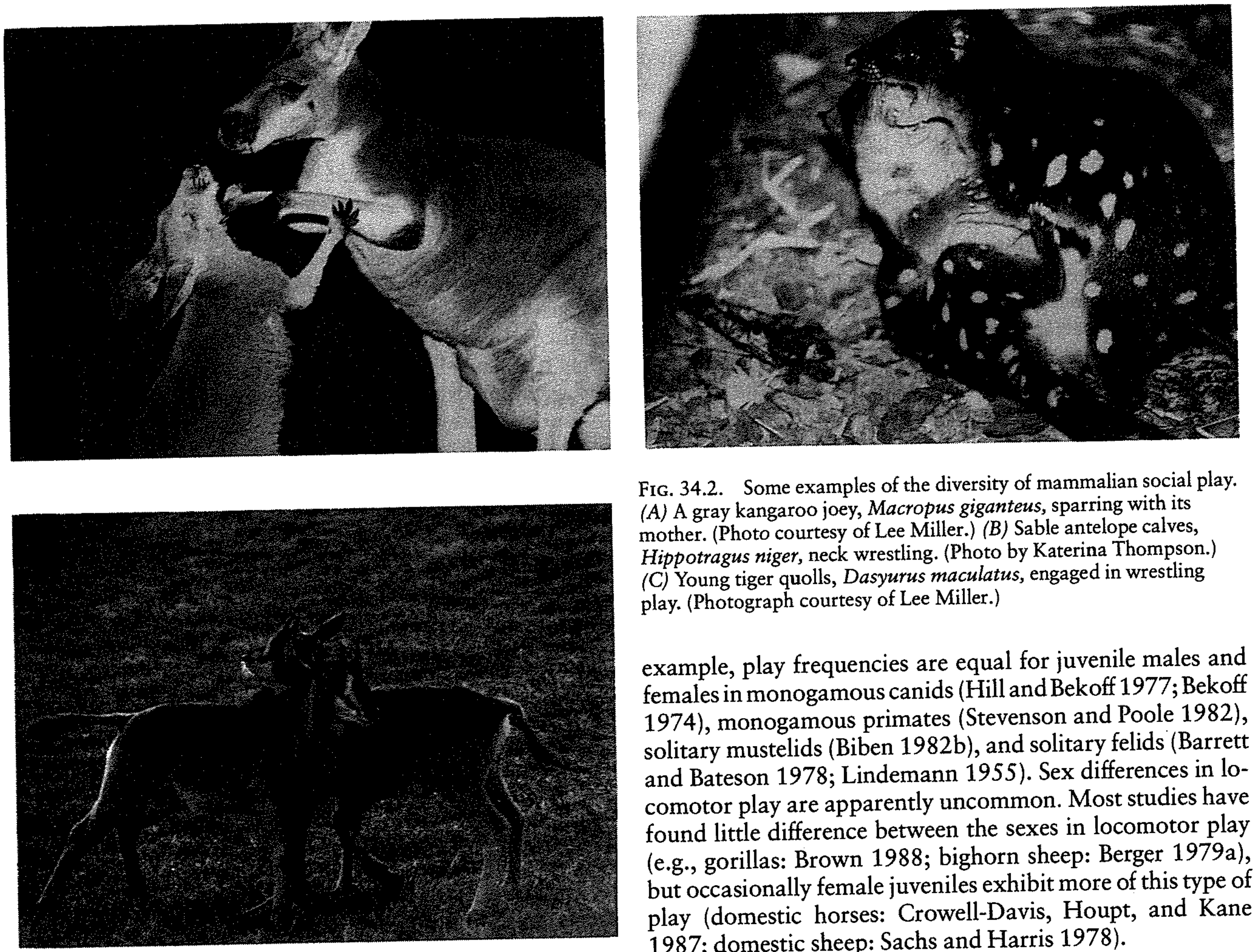

FIG. 34.2. Some examples of the diversity of mammalian social play. *(A)* A gray kangaroo joey, *Macropus giganteus*, sparring with its mother. (Photo courtesy of Lee Miller.) *(B)* Sable antelope calves, *Hippotragus niger*, neck wrestling. (Photo by Katerina Thompson.) *(C)* Young tiger quolls, *Dasyurus maculatus*, engaged in wrestling play. (Photograph courtesy of Lee Miller.)

aggressive behavior. Sex differences in juvenile play frequency are most common in species in which males must aggressively compete for mates and show much greater frequencies of aggression than females. In species in which frequencies of adult aggression are similar between the sexes, no sex differences have been detected in juvenile play. For example, play frequencies are equal for juvenile males and females in monogamous canids (Hill and Bekoff 1977; Bekoff 1974), monogamous primates (Stevenson and Poole 1982), solitary mustelids (Biben 1982b), and solitary felids (Barrett and Bateson 1978; Lindemann 1955). Sex differences in locomotor play are apparently uncommon. Most studies have found little difference between the sexes in locomotor play (e.g., gorillas: Brown 1988; bighorn sheep: Berger 1979a), but occasionally female juveniles exhibit more of this type of play (domestic horses: Crowell-Davis, Houpt, and Kane 1987; domestic sheep: Sachs and Harris 1978).

Where play is sexually dimorphic, differences are manifested in virtually all aspects of play, including frequency, content, ontogeny, and play partner preferences. Juvenile males of a wide variety of species have been reported to play more frequently than females (Meaney, Stewart, and Beatty 1985) and more roughly, using more play patterns involving physical contact (squirrel monkeys: Biben 1986; Siberian ibex, *Capra sibirica:* Byers 1980; rhesus macaques: Symons 1978; baboons: Owens 1975b). Males may exhibit social play earlier in ontogeny than their female siblings (punaré: Thompson 1985) and may continue playing later in development (cercopithecine primates: Bramblett and Coehlo 1987; Symons 1978). Juvenile males often seek out other juvenile males as play partners, presumably because they are more playful than females and provide opportunities to engage in more vigorous play (patas monkeys, *Erythrocebus patas:* Loy and Loy 1987; squirrel monkeys: Biben 1986; Siberian ibex: Byers 1980). Furthermore, male juveniles seem to seek out more varied play experiences, playing more often with adults (rhesus macaques: Breuggeman 1978) and unrelated individuals (Japanese macaques, *Macaca fuscata:* Koyama 1985).

Social and Environmental Factors Affecting Play

Social Factors. Group size influences play by affecting the number and proximity of potential playmates. Play is usually facilitated in large social groups since they are more likely to contain cohorts of similarly aged immature animals. Play is more frequent in large groups of squirrel monkeys than in small groups (Baldwin and Baldwin 1977, 1971). In bighorn sheep lambs, play becomes more complex with increasing group size (Berger 1979a). While increasing group size generally has a positive effect on play, overcrowding may have an inhibitory effect (cats: Leyhausen 1979).

The composition of the social group or peer group also influences juvenile play. The sex ratio of the litter or peer group may be an important factor, especially in species in which play is sexually dimorphic. For example, in the punaré, the age at which social play first appears in both male and female infants is correlated with the proportion of males in the litter: litters with more males begin to play at an earlier age (Thompson 1985). The play of domestic kittens is similarly affected by litter sex ratio, with female kittens from litters containing no males showing significantly less object play than those from mixed-sex litters (Bateson and Young 1979; Barrett and Bateson 1978). Play content may be similarly affected by cohort sex ratio. Female juveniles in cohorts containing many males may show rougher social play than females with fewer male playmates.

The particular individuals with which a juvenile initiates social play are determined by a multitude of factors, many of which have yet to be identified. Relatedness, age disparity, and dominance rank within the social group all influence a juvenile's opportunities to play and its choice of play partners. Kin generally are more likely to play together than are unrelated individuals (Japanese macaques: Glick et al. 1986; Koyama 1985; domestic pigs: Dobao, Rodriganez, and Silio 1984/85; Siberian ibex: Byers 1980; bighorn sheep: Berger 1979a). Play partners of similar ages are also strongly preferred (sable antelope: Thompson 1992; bighorn sheep: Berger 1980; Siberian ibex: Byers 1980; rhesus macaques: Breuggeman 1978;). In twin-bearing primates, play between twins, which are both closely related and identically aged, is by far the most common form of social play (Stevenson and Poole 1982; Izawa 1978; Vogt, Carlson, and Menzel 1978).

Species differ with respect to the sensitivity of social play to differences in social rank. In many primate species, offspring of high-ranking females play more often than offspring of low-ranking females (Breuggeman 1978; Cheney 1978; Gard and Meier 1977), although Symons (1978) reported that the daughter of the highest-ranking rhesus macaque in his study group seldom played and that her play solicitations were largely ignored by her peers. In coyotes, *Canis latrans,* dominance rank among pups is determined by fighting prior to the emergence of social play. Coyote pups in the middle of the dominance hierarchy play more and are more successful in soliciting play than are their high- and low-ranking siblings (Vincent and Bekoff 1978).

Environmental Factors. Food availability is known to have a profound effect on play. Baldwin and Baldwin (1973, 1974) reported that social play was virtually extinguished in a free-ranging population of squirrel monkeys during a period of extreme food scarcity. Subsequent laboratory investigations confirmed that play frequencies in this species were significantly depressed both by limited quantities and by decreased accessibility of food resources (Baldwin and Baldwin 1976). Similar effects have been documented in free-ranging rhesus macaques (Loy 1970), chacma baboons, *Papio ursinus* (Hall 1963), vervet monkeys (Lee 1984), and caribou, *Rangifer tarandus* (Müller-Schwarze and Müller-Schwarze 1982) and in captive rhesus macaques (Oakley and Reynolds 1976) and white-tailed deer (Müller-Schwarze, Stagge, and Müller-Schwarze 1982). Play also appears to be sensitive to the quality of the diet. In vervet monkeys inhabiting a seasonally fluctuating environment, play frequency was correlated with food quality: when the caloric content and the amount of protein in the diet declined, play decreased dramatically (Lee 1984).

Although play frequency is severely affected by food scarcity, this effect is only temporary. In fact, when the quality and quantity of food resources are restored to favorable levels, play rebounds, often reaching frequencies higher than exhibited prior to periods of food scarcity (vervet monkeys: Lee 1984; rhesus macaques: Oakley and Reynolds 1976). This finding suggests that juveniles may be able to compensate for brief periods of play deprivation by increasing subsequent play frequencies, in effect "making up for" lost play time.

Play is inhibited by extremes of temperature. In very cold weather, squirrel monkeys forgo play, preferring instead to bask in the sun (Baldwin 1967). Similarly, in domestic cattle, *Bos taurus,* play ceases when it is cold and wet (Brownlee 1954). Play also tends to decrease when it is very hot. An inverse relationship between the frequency of play and ambient temperature has been reported in domestic horse foals (Crowell-Davis, Houpt, and Kane 1987), northern elephant seals, *Mirounga angustirostris* (Rasa 1971), and rhesus macaques (Oakley and Reynolds 1976). Apparently, extremely cold weather causes juveniles to forgo play in order to conserve the energy needed to maintain a constant body temperature. Vigorous play in extremely hot weather may result in the production of more body heat than the juvenile can easily dissipate.

Play is often facilitated in habitats with certain specific features. Play in several species of ungulates is concentrated on grassy slopes, sandbowls, and snowfields (Berger 1980; Altmann 1956; Darling 1937). Collared peccaries play preferentially on well-worn, scent-marked "playgrounds" near bedding sites (Byers 1985), and play bouts occurring there involve more individuals and last longer than play bouts in other locations. Sandboxes, where a great deal of scent marking occurs, are the preferred sites for locomotor play in captive salt desert cavies, *Dolichotis salinicola* (Wilson and Kleiman 1974). The physical attributes that make these locations popular sites for play have yet to be identified, but perhaps they are places that are relatively safe from predation and where the risk of injury is low.

Play is sometimes inhibited in environments that present too great a risk of injury. Desert bighorn sheep frequently come into contact with the spines of the cholla cactus, *Opuntia* spp., no doubt a painful experience. Lambs in habitats where these cacti are plentiful show much lower rates of play than lambs in grassy habitats (Berger 1980, 1979a).

Not surprisingly, sick animals play less than healthy ones (Fagen 1981), and lack of play may be one of the first symptoms of illness. Gaughan (1983) reported the case of a captive snow leopard female who, in contrast to others studied, rarely played with her cubs. Her lack of play was noted by observers well before the appearance of more obvious signs of illness, such as lethargy and loss of appetite. Medical examination revealed the animal to be seriously ill. Heavy parasite infestation may similarly inhibit play (bighorn sheep: Bennett and Fewell 1987; elk, *Cervus (=canadensis) elaphus:* Altmann 1952).

Captivity. Captivity, which produces profound changes in an animal's immediate physical and social environment, often has significant effects on play. In general, play is more frequent in captive animals than in their free-ranging counterparts. For example, Stevenson and Poole (1982) observed common marmosets, *Callithrix jacchus,* in a free-ranging Brazilian population and in a laboratory colony, and noted that social play was much more frequent in captivity. The higher rates of play seen among captive animals are commonly attributed to unlimited food resources and the absence of predators (Shoemaker 1978).

Adult animals, in particular, seem to show more play in captivity (Fagen 1981). Fagen (1981) suggested that this might represent a reversion to a more infantile state, since in captivity virtually all of an animal's needs are provided for. Alternatively, he proposed that play in adult captives might provide a means of maintaining a healthy physical condition in an environment where opportunities for vigorous exercise are otherwise absent. Captive animals have no need to flee from danger and a reduced need to search actively for food; therefore play might be a captive animal's only means of staying fit and active.

Since play is sensitive to so many social and environmental factors, its presence or absence in captive individuals can be used as an index of the adequacy of the captive environment. Observations of far too little play have indeed been the impetus for reevaluation of the appropriateness of exhibit substrates, the quantity of shade, and herd parasite load in at least one zoo (Bennett and Fewell 1987).

It is desirable to provide captive animals with ample opportunities for play. Playing animals are highly visible to zoo visitors and are likely to hold a visitor's attention for a longer period of time. Also, several studies have shown that exhibit modifications that increase the amount of time captive animals spend playing often result in substantial decreases in abnormal behaviors (e.g., chimpanzees: Paquette and Prescott 1988). Play experience has further been shown to lessen the damaging effects of early social deprivation in rats (Potegal and Einon 1989; Einon, Morgan, and Kibbler 1978).

Some objects and exhibit modifications that promote play in captive animals are listed in table 34.7 (see also Maple and Perkins, chap. 21, this volume). The most important features of play objects are novelty and the ability to stimulate multiple senses (Kieber 1990; Paquette and Prescott 1988; Hutt 1967). Rotating play objects among different enclosures is a highly effective way of preserving their appeal (Kieber 1990; Paquette and Prescott 1988). If preserving the natural appearance of the exhibit is a primary objective, conspicuously man-made play objects can be restricted to off-exhibit areas (Kieber 1990).

The enigmatic nature of the function of play makes it extremely difficult to assess whether immature animals in captive environments are obtaining adequate amounts and types of play experience. Perhaps the most conservative approach to ensuring optimal juvenile development is to attempt to mimic natural social groupings and features of the native habitat such that opportunities for locomotor, object, and social play are as similar as possible to those of free-ranging animals. All captive immature animals should be provided with enough space to engage in vigorous locomotor play, a variety of objects to manipulate, and conspecifics, preferably of similar ages, with which to engage in social play. Allowing access to a wide range of play experiences may be the best way to ensure that captive animals do not suffer physiological and behavioral deficits as a result of their somewhat artificial upbringing.

CONCLUSIONS

Evidence exists that deficits in early development (most notably social development) have far-reaching and often permanent consequences. The best way to promote normal behavioral development is to allow infants to be mother-reared in a diverse and spacious physical environment and in a social environment that closely approximates that in the wild. When mother-rearing is not possible, other alternatives, in order of their desirability, are (1) using another lactating female as a foster mother, (2) hand-rearing the infant without removing it from the social group, and (3) hand-rearing the infant with conspecific peers. Hand-rearing infants in isolation should be considered a last resort, and the techniques of artificial rearing should be based on the normal developmental patterns of the species in question (Collier 1983). Understanding the natural course of development in each mammalian species is critical for ensuring that captive-born infants grow into competent adults.

TABLE 34.7. Methods of Promoting Play Behavior in Captive Mammals

Taxonomic group	Exhibit modification or addition	Type of play promoted	References
Ungulates	Open space	Locomotor	
	Hills, sloped surfaces, rock piles	Locomotor and social	
Carnivores	Wooden balls, leather balls, sticks, stones, logs, tires, cardboard boxes, large paper bags, hanging rope, plasic jugs (with lids removed), rawhide bones, beef bones	Object	Kieber 1990; Biben 1982a; Hediger 1968
	PVC tubing	Locomotor	Biben 1982b
Rhinos and elephants	Planks, stumps, blocks of wood	Object	Hediger 1968
Aquatic mammals	Pieces of floating wood, blocks of ice with embedded fish	Object	Sanders 1987; Hediger 1968
Monkeys	Networks of branches with flexible attachment points, hanging milk crates, rope swings	Locomotor	Clark 1990; Hutchins, Hancocks, and Crockett 1978
	Nylon balls	Object	Renquist and Judge 1985
Great apes	Tire swings	Locomotor	Paquette and Prescott 1988
	Loose tires, burlap feed bags, heavy rubber feed tubs, heavy plastic drums (cut in half), straw or hay, branches, rubber balls	Object	Cole 1987; Goerke, Fleming, and Creel 1987; Cole and Ervine 1983; Sammarco 1981

REFERENCES

Adamson, J. 1960. *Born free.* London: Collins and Harvill Press.

———. 1969. *The spotted sphinx.* London: Collins and Harvill Press.

Altmann, J. 1978. Infant independence in yellow baboons. In *The development of behavior: Comparative and evolutionary aspects,* ed. G. M. Burghardt and M. Bekoff, 253–77. New York: Garland STPM Press.

Altmann, M. 1952. Social behavior of elk, *Cervus canadensis nelsoni,* in the Jackson Hole area of Wyoming. *Behaviour* 4:116–43.

———. 1956. Patterns of herd behavior in free-ranging elk of Wyoming. *Zoologica* 41:65–71.

Baldwin, J. D. 1967. A study of the social behavior of a semi-free-ranging colony of squirrel monkeys *(Saimiri sciureus).* Ph.D. thesis, Johns Hopkins University.

———. 1969. The ontogeny of social behavior of squirrel monkeys *(Saimiri sciureus)* in a seminatural environment. *Folia Primatol.* 11:35–79.

———. 1986. Behavior in infancy: Exploration and play. In *Comparative primate biology,* vol. 2A: *Behavior, conservation, and ecology,* 295–326. New York: Alan R. Liss.

Baldwin, J. D., and Baldwin, J. I. 1971. Squirrel monkeys *(Saimiri sciureus)* in natural habitats in Panama, Colombia, Brazil, and Peru. *Primates* 12:45–61.

———. 1973. The role of play in social organization: Comparative observations on squirrel monkeys *(Saimiri). Primates* 14:369–81.

———. 1974. Exploration and social play in squirrel monkeys *(Saimiri). Am. Zool.* 14:303–15.

———. 1976. The effects of food ecology on social play: A laboratory simulation. *Z. Tierpsychol.* 40:1–14.

———. 1977. The role of learning phenomena in the ontogeny of exploration and play. In *Primate bio-social development,* ed. S. Chevalier-Skolnikoff and F. E. Poirier, 343–406. New York: Garland STPM Press.

Banks, D. R. 1978. Hand-rearing a musk-ox at Calgary Zoo. *Int. Zoo Yrbk.* 18:213–15.

Barash, D. P. 1976. Social behavior and individual differences in free living Alpine marmots *(Marmota marmota). Anim. Behav.* 24:27–35.

Barrett, P., and Bateson, P. 1978. The development of play in cats. *Behaviour* 66:106–20.

Bateson, P., and Young, M. 1979. The influence of male kittens on the object play of their female siblings. *Behav. Neural Biol.* 27:374–78.

Beach, F. A. 1939. Maternal behavior of the pouchless marsupial *Marmosa cinerea. J. Mammal.* 20:315–22.

Bekoff, M. 1972. The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *Q. Rev. Biol.* 47:412–34.

———. 1974. Social play and play soliciting by infant canids. *Am. Zool.* 14:323–40.

———. 1976. The social deprivation paradigm: Who's being deprived of what? *Dev. Psychobiol.* 9:497–98.

———. 1985. Evolutionary perspectives of behavioral development. *Z. Tierpsychol.* 69:166–67.

Bennett, B., and Fewell, J. H. 1987. Play frequencies in captive and free-ranging bighorn lambs *(Ovis canadensis canadensis). Zoo Biol.* 6:237–41.

Berger, J. 1979a. Social ontogeny and behavioral diversity: Consequences for Bighorn sheep, *Ovis canadensis,* inhabiting desert and mountain environments. *J. Zool.* (Lond.) 188:251–66.

———. 1979b. Weaning conflict in desert and mountain bighorn sheep *(Ovis canadensis):* An ecological interpretation. *Z. Tierpsychol.* 50:188–200.

———. 1980. The ecology, structure, and functions of social play in bighorn sheep. *J. Zool.* (Lond.) 192:531–42.

———. 1986. *Wild horses of the great basin.* Chicago: University of Chicago Press.

Berman, C. M. 1984. Variation in mother-infant relationships: Traditional and nontraditional factors. In *Female primates: Studies by women primatologists,* ed. M. F. Small, 17–36. New York: Alan R. Liss.

Biben, M. 1982a. Object play and social treatment of prey in bush dogs and crab eating foxes. *Behaviour* 79:201–11.

———. 1982b. Sex differences in the play of young ferrets. *Biol. Behav.* 7:303–8.

———. 1983. Comparative ontogeny of social behavior in three South American canids, the maned wolf, crab eating fox, and bush dog: Implications for sociality. *Anim. Behav.* 31: 814–26.

———. 1986. Individual- and sex-related strategies of wrestling play in captive squirrel monkeys. *Ethology* 71:229–41.

Biben, M., and Symmes, D. 1986. Play vocalizations of squirrel monkeys *(Saimiri sciureus). Folia Primatol.* 46:173–82.

Billing, A. E., and Vince, M. A. 1987a. Teat-seeking behaviour in newborn lambs. I. Evidence for the influence of maternal skin temperature. *Appl. Anim. Behav. Sci.* 18:301–13.

———. 1987b. Teat-seeking behaviour in newborn lambs. II. Evidence for the influence of the dam's surface textures and degree of surface yield. *Appl. Anim. Behav. Sci.* 18:315–25.

Bowen, W. D., Oftedal, O. T., and Boness, D. J. 1985. Birth to weaning in four days: Remarkable growth in the hooded seal, *Cystophora cristata. Can. J. Zool.* 63:2841–46.

Bowker, M. H. 1977. Behavior of Kirk's dik-dik *(Madoqua kirki hindei)* in Kenya. Ph.D. thesis, Northern Arizona University.

Box, H. O. 1975. A social development study of young monkeys *(Callithrix jacchus)* within a captive family group. *Primates* 16: 155–74.

Brainard, L. 1985. *Biological values for selected mammals.* Topeka, Kans.: American Association of Zoo Keepers.

Bramblett, C. A., and Coehlo, A. M. 1987. Development of social behavior in vervet monkeys, Syke's monkeys, and baboons. In *Comparative behavior of African monkeys,* ed. E. L. Zucker, 67–79. New York: Alan R. Liss.

Breuggeman, J. A. 1978. The function of adult play in free-ranging *Macaca mulatta.* In *Social play in primates,* ed. E. O. Smith, 169–92. New York: Academic Press.

Brown, S. G. 1988. Play behavior in lowland gorillas: Age differences, sex differences, and possible functions. *Primates* 29:219–28.

Brownlee, A. 1954. Play in domestic cattle: An analysis of its nature. *Br. Vet. J.* 110:48–68.

Buechner, H. K., Mackler, S. F., Stroman, H. R., and Xanten, W. A. 1975. Birth of an Indian rhinoceros, *Rhinoceros unicornis,* at the National Zoological Park, Washington. *Int. Zoo Yrbk.* 15: 160–65.

Burghardt, G. M. 1984. On the origins of play. In *Play in animals and humans,* ed. P. K. Smith, 5–41. New York: Blackwell.

———. 1988. Precocity, play, and the ectotherm-endotherm transition: Profound reorganization or superficial adaptation? In *Handbook of behavioral neurobiology,* vol. 9, ed. E. M. Blass, 107–48. New York: Plenum.

Byers, J. A. 1980. Play partner preference in Siberian ibex, *Capra ibex siberica. Z. Tierpsychol.* 53:23–40.

———. 1984. Ungulate play behavior. In *Play in animals and humans,* ed. P. K. Smith, 43–65. New York: Blackwell.

———. 1985. Olfaction-related behavior in collared peccaries. *Z. Tierpsychol.* 70:201–10.

Carr, W. J., Marasco, E., and Landauer, M. R. 1979. Responses by rat pups to their own nest verses a strange conspecific nest. *Physiol. Behav.* 23:1149–51.

Chalmers, N. R. 1980. The ontogeny of play in feral olive baboons *(Papio anubis). Anim. Behav.* 28:570–95.

Charles-Dominique, P. 1977. *Ecology and behavior of nocturnal primates: Prosimians of equatorial West Africa.* New York: Columbia University Press.

Cheney, D. L. 1978. Play partners of immature baboons. *Anim. Behav.* 26:1038–50.

Clark, B. 1990. Environmental enrichment: An overview of theory and application for captive non-human primates. *Animal Keepers' Forum* 17:272–82.

Clark, C. B. 1977. A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In *Primate biosocial development,* ed. S. Chevalier-Skolnikoff and F. E. Poirier, 235–60. New York: Garland.

Cleveland, J., and Snowdon, C. T. 1984. Social development during the first twenty weeks in the cotton-top tamarin *(Saguinus o. oedipus). Anim. Behav.* 32:432–44.

Cole, M. 1987. How we keep our gorillas occupied. *Animal Keepers' Forum* 14:401–3.

Cole, M., and Ervine, L. 1983. Maternal behavior and infant development of the lowland gorillas at Metro Toronto Zoo. *Animal Keepers' Forum* 10:387–91.

Collier, C. E. 1983. The distorted mirror: Avoiding abnormal behavior in hand reared mammals. *AAZPA Annual Conference Proceedings,* 233–34. Wheeling, W.Va.: American Association of Zoological Parks and Aquariums.

Croft, D. B. 1981. Social behaviour of the euro, *Macropus robustus,* in the Australian arid zone. *Aust. J. Wildl. Res.* 8: 13–49.

Crowell-Davis, S. L. 1986. Spatial relations between mare and foals of the Welsh pony *(Equus caballus). Anim. Behav.* 34: 1007–15.

Crowell-Davis, S. L., and Houpt, K. 1985. Coprophagy by foals: Effect of age and possible functions. *Equine Vet. J.* 17:17–19.

Crowell-Davis, S. L., Houpt, K. A., and Kane, L. 1987. Play development in Welsh pony *(Equus caballus)* foals. *Appl. Anim. Behav. Sci.* 18:119–31.

Dane, B. 1977. Mountain goat social behavior: Social structure and "play" behavior as affected by dominance. In *Proceedings of the First International Mountain Goat Symposium,* ed. W. M. Samuel and W. G. Macgregor, 92–106. British Columbia: Ministry of Recreation and Conservation.

Darling, F. F. 1937. *A herd of red deer.* London: Oxford University Press.

Davies, V. A., and Kemble, E. D. 1983. Social play and insect predation in northern grasshopper mice *(Onychomys leucogaster). Behav. Proc.* 8:197–204.

DeGhett, V. J. 1978. The ontogeny of ultrasound production in rodents. In *The development of behavior: Comparative and evolutionary aspects,* ed. G. M. Burghardt and M. Bekoff, 253–77. New York: Garland STPM Press.

Dobao, O. M. T., Rodriganez, J., and Silio, L. 1984/85. Choice of companions in social play in piglets. *Appl. Anim. Behav. Sci.* 13: 259–66.

Dunbar, R. I. M. 1980. Determinants and evolutionary consequences of dominance among female gelada baboons. *Behav. Ecol. Sociobiol.* 7:253–65.

———. 1984. *Reproductive decisions: An economic analysis of gelada baboon social strategies.* Princeton, N.J.: Princeton University Press.

Eadie, M. J., and Mann, S. W. 1970. Development and instability of rumen microbial populations. In *Physiology of digestion and metabolism in the ruminant,* ed. A. T. Phillipson, 335–47. Newcastle-Upon-Tyne, England: Oriel Press.

Edwards, J. 1976. Learning to eat by following the mother in moose calves. *Am. Midland Nat.* 96:229–32.

Ehret, G., and Berndecker, C. 1986. Low-frequency sound communication by mouse pups *(Mus musculus):* Wriggling calls release maternal behaviour. *Anim. Behav.* 34:821–30.

Eibl-Eibesfeldt, I. 1950. On the ontogeny of behavior of a male badger (*Meles meles* L.) with particular reference to play behavior. *Z. Tierpsychol.* 7:345–51.

Einon, D. F., Morgan, M. J., and Kibbler, C. C. 1978. Brief periods of socialization and later behaviour in the rat. *Dev. Psychobiol.* 11:213–25.

Eisenberg, J. F. 1981. *The mammalian radiations: An analysis of trends in evolution, adaptation, and behavior.* Chicago: University of Chicago Press.

Eltringham, S. K. 1982. *Elephants.* Dorset, England: Blanford Press.

Espmark, Y. 1969. Mother-young relations and development of behavior in roe deer (*Capreolus capreolus* L.). *Viltrevy* 6:462–540.

———. 1971. Mother-young relationship and ontogeny of behavior in reindeer (*Rangifer tarandus,* L.). *Z. Tierpsychol.* 29:42–81.

Estes, R. D. 1976. The significance of breeding synchrony in the wildebeest. *E. Afr. Wildl. J.* 14:135–52.

Estes, R. D., and R. K. Estes. 1979. The birth and survival of wildebeest calves. *Z. Tierpsychol.* 50:45–95.

Ewer, R. F. 1959. Suckling behaviour in kittens. *Behaviour* 15: 146–62.

———. 1968. *Ethology of mammals.* New York: Plenum.

———. 1973. *The carnivores.* Ithaca, N.Y.: Cornell University Press.

Ewer, R. F., and Wemmer, C. 1974. The behaviour in captivity of the African civet, *Civettictis civetta* (Schreber). *Z. Tierpsychol.* 34:359–94.

Fagen, R. 1976. Exercise, play, and physical training in animals. In *Perspectives in ethology,* ed. P. P. G. Bateson and P. H. Klopfer, 189–219. New York: Plenum.

———. 1981. *Animal play behavior.* New York: Oxford University Press.

Fairbanks, L. A., and McGuire, M. T. 1985. Relationships of vervet mothers with sons and daughters from one through three years of age. *Anim. Behav.* 33:40–50.

Farentinos, R. C. 1971. Some observations on the play behavior of the Stellar sea lion *(Eumetopias jubata). Z. Tierpsychol.* 28: 428–38.

Ferron, J. 1981. Comparative ontogeny of behaviour in four species of squirrels (Sciuridae). *Z. Tierpsychol.* 55:192–216.

Fox, M. W., Halperin, S., Wise, A., and Kohn, E. 1976. Species and hybrid differences in frequencies of play and agonistic actions in canids. *Z. Tierpsychol.* 40:194–209.

Frädrich, H., and Thenius, E. 1972. Tapirs. In *B. Grzimek's animal life encyclopedia,* vol. 13, 17–33. New York: Van Nostrand Reinhold.

Galef, B. J. 1981. The ecology of weaning: Parasitism and the achievement of independence by altricial animals. In *Parental behavior in mammals,* ed. D. J. Gubernick and P. H. Klopfer, 211–41. New York: Plenum.

Gard, G. C., and Meier, G. W. 1977. Social and contextual factors of play behavior in sub-adult rhesus monkeys. *Primates* 18: 367–77.

Gaughan, M. M. 1983. Play and infant development reflecting on mother-rearing in the captive snow leopard *(Panthera uncia). AAZPA Regional Conference Proceedings,* 589–98. Wheeling, W.Va.: American Association of Zoological Parks and Aquariums.

Gauthier, D., and Barrette, C. 1985. Suckling and weaning in captive white-tailed deer and fallow deer. *Behaviour* 94:128–49.

Gentry, R. L. 1974. The development of social behavior through play in the Stellar sea lion. *Am. Zool.* 14:391–403.

Glick, B. B., Eaton, G. G., Johnson, D. F., and Worlein, J. 1986. Development of partner preferences in Japanese macaques *(Macaca fuscata):* Effects of gender and kinship during the second year of life. *Int. J. Primatol.* 7:467–79.

Goedeking, P. 1985. Zur Kovariation von Lautstrukturvariabilitaten und sozialem Spiel bei Lisztaffen *(Saguinus oedipus oedipus):* Gesteuerte Lautanalysemethoden. Ph.D. thesis, Universität Bielefeld.

Goerke, B., Fleming, L., and Creel, M. 1987. Behavioral changes of a juvenile gorilla after a transfer to a more naturalistic environment. *Zoo Biol.* 8:283–95.

Gomendio, M. 1988. The development of different types of play in gazelles: Implications for the nature and functions of play. *Anim. Behav.* 36:825–36.

Goodall, J. 1986. *The chimpanzees of Gombe: Patterns of behavior.* Cambridge, Mass.: Belknap Press of Harvard University Press.

Gould, E., and Bres, M. 1986. Regurgitation and reingestion in captive gorillas: Description and intervention. *Zoo Biol.* 5:241–50.

Griffiths, M. 1968. *Echidnas.* Oxford: Pergamon Press.

Guy, P. R. 1977. Coprophagy in the African elephant (*Loxodonta africana* Blumenbach). *E. Afr. Wildl. J.* 15:174.

Hall, K. R. L. 1963. Variations in the ecology of the chacma baboon *(Papio ursinus). Symp. Zool. Soc. Lond.* 10:1–28.

Hall, W. G., and Williams, C. L. 1983. Suckling isn't always feeding, or is it? A search for developmental continuities. *Adv. Stud. Behav.* 13:219–54.

Happold, M. 1976. The ontogeny of social behaviour in four conilurine rodents (Muridae) of Australia. *Z. Tierpsychol.* 40:265–78.

Harlow, H. F., and Harlow, M. K. 1969. Effects of various mother-infant relationships on rhesus monkey behaviors. *Determinants of Infant Behavior* 4:15–36.

Hartman, D. 1979. *Ecology and behavior of the manatee* (Trichechus manatus) *in Florida.* Special Publication no. 5. Lawrence, Kans.: American Society of Mammalogists.

Hauser, M. D. 1986. Parent-offspring conflict: Care elicitation behaviour and the "cry-wolf" syndrome. In *Primate ontogeny, cognition, and social behaviour,* ed. J. G. Else and P. C. Lee, 193–203. Cambridge: Cambridge University Press.

Hauser, M. D., and Fairbanks, L. A. 1988. Mother-offspring conflict in vervet monkeys: Variation in response to ecological conditions. *Anim. Behav.* 36:802–13.

Hayaki, H. 1985. Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates* 26:343–60.

Hediger, H. 1968. *The psychology and behavior of animals in zoos and circuses.* New York: Dover.

Hemmer, H. 1972. *Uncia uncia. Mammal. Species* 20:1–5.

Hendy, H. 1986. Social interactions of free-ranging baboon infants. In *Primate ontogeny, cognition, and social behaviour,* ed. J. G. Else and P. C. Lee, 267–80. Cambridge: Cambridge University Press.

Henry, J. D., and Herrero, S. M. 1974. Social play in the American black bear. *Am. Zool.* 14:371–89.

Hepper, P. G. 1983. Sibling recognition in the rat. *Anim. Behav.* 31:1177–91.

Herrmann, D. 1971. Beobachtungen des Gruppenlebens ostaustralischer Graugrosskanguruhs, *Macropus giganteus* (Zimmerman, 1977) und Bennetkanguruhs, *Protemnodon rufogrisea* (Demarest, 1817). *Säugetierk. Mitt.* 19:352–62.

Hill, H. L., and Bekoff, M. 1977. The variability of some motor components of social play and agonistic behaviour in infant coyotes, *Canis latrans. Anim. Behav.* 25:907–9.

Hinde, R. A. 1977. Mother-infant separation and the nature of inter-individual relationships: Experiments with rhesus monkeys. *Proc. R. Soc. Lond.* B 196:29–50.

Hinde, R. A., and Spencer-Booth, Y. 1967. The behaviour of socially living rhesus monkeys in their first two and a half years. *Anim. Behav.* 15:183–200.

Hoage, R. J. 1977. Parental care in *Leontopithecus rosalia rosalia:*

Sex and age differences in carrying behavior and the role of prior experience. In *The biology and conservation of the Callitrichidae,* ed. D. G. Kleiman, 293–305. Washington, D.C.: Smithsonian Institution.

———. 1982. *Social and physical maturation in captive lion tamarins,* Leontopithecus rosalia rosalia *(Primates: Callitrichidae).* Smithsonian Contributions to Zoology, no. 354. Washington, D.C.: Smithsonian Institution Press.

Hrdy, S. B. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Adv. Stud. Behav.* 6:101–58.

Hudson, R., and Distel, H. 1985. Nipple location by newborn rabbits: Behavioural evidence for pheromonal guidance. *Behaviour* 85:260–75.

Hungate, R. E. 1968. Ruminal fermentation. In *Handbook of physiology,* vol. 5, *Alimentary canal,* ed. C. F. Cade, 2725–45. Washington, D.C.: American Physiological Society.

Hutchins, M., Hancocks, D., and Crockett, C. 1978. Naturalistic solutions to the behavioral problems of captive animals. *AAZPA Annual Conference Proceedings,* 108–13. Wheeling, W.Va.: American Association of Zoological Parks and Aquariums.

Hutt, C. 1967. Temporal effects on response decrement and stimulus satiation in exploration. *Br. J. Psychol.*58:365–73.

Izawa, K. 1978. A field study of the ecology and behavior of the black-mantle tamarin *(Saguinus nigricollis). Primates* 19:241–74.

Jamieson, S. H., and Armitage, K. B. 1987. Sex differences in the play behavior of yearling yellow-bellied marmots. *Ethology* 74: 237–53.

Jensen, G. D., Bobbitt, R. A., and Gordon, B. N. 1968. Sex differences in development of independence of infant monkeys. *Behaviour* 30:1–14.

Johnsingh, A. J. T. 1982. Reproductive and social behaviour of the dhole, *Cuon alpinus* (Canidae). *J. Zool.* (Lond.) 198:443–63.

Jolly, A. 1972. *The evolution of primate behavior.* New York: Macmillan.

Jungius, H. 1971. *The biology and behavior of the reedbuck (*Redunca arundinum *Boddaert 1785) in the Kruger National Park.* Hamburg: Paul Parey.

Kaufmann, J. H. 1974. Social ethology of the whiptail wallaby, *Macropus parryi,* in northeastern New South Wales. *Anim. Behav.* 22:281–369.

———. 1975. Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus. Anim. Behav.* 23: 214–21.

Kieber, C. 1990. Behavioral enrichment for felines in holding areas. *AAZPA Regional Conference Proceedings,* 585–89. Wheeling, W.Va.: American Association of Zoological Parks and Aquariums.

Kleiman, D. G. 1972. Maternal behavior of the green acouchi *(Myoprocta pratti),* a South American caviomorph rodent. *Behaviour* 43:48–84.

Kleiman, D. G., and Malcolm, J. R. 1981. The evolution of male parental investment in mammals. In *Parental care in mammals,* ed. D. J. Gubernick and P. H. Klopfer, 347–87. New York: Plenum.

Kovach, J. K., and Kling, A. 1967. Mechanisms of neonate sucking behaviour in the kitten. *Anim. Behav.* 15:91–101.

Koyama, N. 1985. Playmate relationships among individuals of the Japanese monkey troop in Arashiyama. *Primates* 26:390–406.

Lawick-Goodall, J. Van. 1967. Mother-offspring relationships in free-ranging chimpanzees. In *Primate ethology,* ed. D. Morris, 287–346. Chicago: Aldine.

———. 1968. The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.* 1:161–311.

———. 1971. *In the shadow of man.* Boston: Houghton Mifflin.

Lee, P. C. 1984. Ecological constraints on the social development of vervet monkeys. *Behaviour* 93:245–62.

Lee, P. C., and Moss, C. J. 1986. Early maternal investment in male and female elephant calves. *Behav. Ecol. Sociobiol.* 18:353–61.

Lekagul, B., and McNeely, J. A. 1977. *Mammals of Thailand.* Bangkok: Sahakarnbhat.

Lent, P. C. 1974. Mother-infant relationships in ungulates. In *The behavior of ungulates and its relation to management,* ed. V. Geist and F. Walther, 14–55. Morges, Switzerland: IUCN Publications.

Leon, M. 1975. Dietary control of maternal pheromone in the lactating rat. *Physiol. Behav.* 14:311–19.

Leresche, L. A. 1976. Dyadic play in hamadryas baboons. *Behaviour* 57:190–205.

Leuthold, W. 1977. *African ungulates: A comparative review of their ethology and behavioral ecology.* Berlin: Springer-Verlag.

Leyhausen, P. 1965. Über die Funktion der relativen Stimmungshierarchie (dangestellt am Beispiel der phylogenetischen und ontogenetischen Entwicklung des Beutefangs von Raubtieren). *Z. Tierpsychol.* 22:412–94.

———. 1979. *Cat behavior.* New York: Garland STPM Press.

Lickliter, R. E. 1984. Hiding behavior in domestic goat kids. *Appl. Anim. Behav. Sci.* 12:245–51.

Lindemann, W. 1955. Über die Jugendentwicklung beim Luchs (*Lynx l. lynx* Kerr) und bei der Wildkatze (*Felis s. sylvestris* Schreb.). *Behaviour* 8:1–45.

Lohmer, R. 1976. Zur Verhaltensontogenese bei *Procyon cancrivorus* (Procyonidae). *Z. Säugetierk.* 41:42–58.

Loizos, C. 1966. Play in mammals. *Symp. Zool. Soc. Lond.* 18:1–9.

Loy, J. 1970. Behavioral responses of free-ranging rhesus monkeys to food shortage. *Am. J. Phys. Anthropol.* 33:263–71.

Loy, K. M., and Loy, J. 1987. Sexual differences in early social development among captive patas monkeys. In *Comparative behavior of African monkeys,* ed. E. L. Zucker, 23–37. New York: Alan R. Liss.

MacKinnon, J. 1974. The behavior and ecology of wild orangutans *(Pongo pygmaeus). Anim. Behav.* 22:3–74.

Maple, T. 1980. *OrangUtan Behavior.* New York: Van Nostrand Reinhold.

Maple, T., and Zucker, E. L. 1978. Ethological studies of play behavior in captive great apes. In *Social play in primates,* ed. E. O. Smith, 113–42. New York: Academic Press.

Martin, P. 1984. The (four) whys and wherefores of play in cats: A review of functional, evolutionary, developmental, and causal issues. In *Play in animals and humans,* ed. P. K. Smith, 159–73. New York: Blackwell.

Martin, P., and Caro, T. M. 1985. On the functions of play and its role in behavioral development. *Adv. Stud. Behav.* 15:59–103.

Martin, R. D. 1968. Reproduction and ontogeny in tree shrews *(Tupaia belangeri),* with reference to their general behaviour and taxonomic relationships. *Z. Tierpsychol.* 25:409–532.

Martin, R. W., and Lee, A. 1984. *Possums and gliders.* Chipping Norton, N.S.W., Australia: Surrey Beatty and Son.

McVittie, R. 1978. Nursing behaviour of snow leopard cubs. *Appl. Anim. Ethol.* 4:159–68.

Meaney, M. J., Stewart, J., and Beatty, W. W. 1985. Sex differences in social play: The socialization of sex roles. *Adv. Stud. Behav.* 15:1–58.

Meissner, K., and Ganslosser, U. 1985. Ontogeny of social behaviour of the kowari, *Dasyuroides byrnei* Spencer, 1896 (Marsupialia: Dasyuridae). I. A comparison of the behavioural repertoire of juvenile and adult kowaris. *Zool. Anz., Jena* 214:291–308.

Melnick, D. J., and Pearl, M. C. 1987. Cercopithecines in multimale groups: Genetic diversity and population structure. In *Pri-*

mate societies, ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, 121–34. Chicago: University of Chicago Press.

Mendoza, S. P., and Mason, W. A. 1986. Parental division of labour and differentiation of attachments in a monogamous primate *(Callicebus moloch). Anim. Behav.* 34:1336–47.

Mohr, E. 1968. Spielbereitschaft bei Wisent. *Z. Säugetierk.* 33: 116–21.

Müller-Schwarze, D., and Müller-Schwarze, C. 1982. Play behaviour in free-ranging caribou *Rangifer tarandus. Acta Zoologica Fennica* 175:121–24.

Müller-Schwarze, D., Stagge, B., and Müller-Schwarze, C. 1982. Play behavior: Persistence, decrease, and energetic compensation during food shortage in deer fawns. *Science* 215:85–87.

Nash, L. T. 1978. The development of the mother-infant relationship in wild baboons *(Papio anubis). Anim. Behav.* 28:746–59.

Nelson, T. A., and Woolf, A. 1987. Mortality of white-tailed deer fawns in southern Illinois. *J. Wildl. Mgmt.* 51:326–29.

Niemitz, C. 1974. A contribution to the postnatal behavioral development of *Tarsius bancanus,* Horsfield, 1821, studied in two cases. *Folia Primatol.* 21:250–76.

Nowak, R. M., and Paradiso, J. L. 1983. *Walker's mammals of the world.* Baltimore: Johns Hopkins University Press.

Oakley, F. B., and Reynolds, P. C. 1976. Differing responses to social play deprivation in two species of macaque. In *The anthropological study of play: Problems and perspectives,* ed. D. F. Lancy and B. A. Tindall, 179–88. Cornwall, N.Y.: Leisure Press.

Oftedal, O. T. 1980. Milk composition and formula selection for hand-rearing young mammals. *Proceedings of the First Annual Dr. Scholl Nutrition Conference: A Conference on the Nutrition of Captive Wild Animals,* ed. E. R. Maschgan, M. E. Allen, and L. E. Fisher, 67–83. Chicago: Lincoln Park Zoological Gardens.

Owens, N. W. 1975a. A comparison of aggressive play and aggression in free living baboons, *Papio anubis. Anim. Behav.* 23: 757–65.

———. 1975b. Social play behavior in free-living baboons, *Papio anubis. Anim. Behav.* 23:387–408.

Owen-Smith, N. 1973. The behavioral ecology of the white rhinoceros. Ph.D. thesis, University of Wisconsin.

———. 1975. The social ethology of the white rhinoceros *Ceratotherium simum. Z. Tierpsychol.* 38:338–84.

Pages, E. 1983. Identification characterisation et role du jeu social chez un prosimien nocturne, *Microcebus coquereli. Biol. Behav.* 8:319–43.

Paquette, D., and Prescott, J. 1988. Use of novel objects to enhance environments of captive chimpanzees. *Zoo Biol.* 7:15–23.

Parker, G. A., and McNair, M. R. 1979. Models of parent-offspring conflict. IV. Suppression: Evolutionary retaliation by the parent. *Anim. Behav.* 27:1210–35.

Patenaude, F. 1983. Care of the young in a family of wild beavers, *Castor canadensis. Acta Zoologica Fennica* 174:121–22.

Pereira, M. E., Klepper, A., and Simons, E. L. 1987. Tactics of care for young infants by forest-living ruffed lemurs *(Varecia variegata variegata):* Ground nests, parking, and biparental guarding. *Am. J. Primatol.* 13:129–44.

Pfeffer, I. 1967. Le mouflon de Corse (*Ovis ammon musimon* Schreber 1782) position systematique ecologie et ethologie comparees. *Mammalia* (suppl.) 31:1–262.

Pfeifer, S. 1980. Role of the nursing order in social development of mountain lion kittens. *Dev. Psychobiol.* 13:47–53.

Poduschka, W. 1969. Erganzungen zum Wissen über *Erinaceus e. roumanicus* und kritische Uberlegungen zur bisherigen Literatur über europaische Igel. *Z. Tierpsychol.* 26:761–804.

Poirier, F. E. 1968. The Nilgiri langur *(Presbytis johnii)* mother-infant dyad. *Primates* 9:45–68.

———. 1970. Nilgiri langur ecology and social behavior. In *Primate behavior: Developments in field and laboratory research,* ed. L. A. Rosenblum, 251–383. New York: Academic Press.

Poole, T. B. 1966. Aggressive play in polecats. *Symp. Zool. Soc. Lond.* 18:23–44.

———. 1978. An analysis of social play in polecats (Mustelidae) with comments on the form and evolutionary history of the open mouth play face. *Anim. Behav.* 26:36–49.

Poole, T. B., and Fish, J. 1975. An investigation of playful behaviour in *Rattus norvegicus* and *Mus musculus. J. Zool. (Lond.)* 175:61–71.

———. 1976. An investigation of individual, age, and sex differences in the play of *Rattus norvegicus. J. Zool. (Lond.)* 179: 249–60.

Potegal, M., and Einon, D. 1989. Aggressive behaviors in adult rats deprived of playfighting experience as juveniles. *Dev. Psychobiol.* 22:159–72.

Priestnall, R. 1983. Postpartum changes in maternal behaviour. In *Parental behaviour of rodents,* ed. R. W. Elwood, 67–93. New York: John Wiley and Sons.

Provenzo, F. D., and Balph, D. F. 1987. Diet learning by domestic ruminants: Theory, evidence, and practical implications. *Appl. Anim. Behav. Sci.* 18:211–32.

Ralls, K., Lundrigan, B., and Kranz, K. 1987a. Mother-young relationships in captive ungulates: Behavioral changes over time. *Ethology* 75:1–14.

———. 1987b. Mother-young relationships in captive ungulates: Spatial and temporal patterns. *Zoo Biol.* 6:11–20.

Rasa, O. E. A. 1971. Social interaction and object manipulation in weaned pups of the Northern elephant seal *Mirounga angustirostris. Z. Tierpsychol.* 32:449–88.

———. 1984. A motivational analysis of object play in juvenile dwarf mongoose *(Helogale undulata rufula). Anim. Behav.* 32: 579–89.

Renouf, D., and Diemand, D. 1984. Behavioral interactions between harbour seal mothers and pups during weaning (Pinnipeds: Phocidae). *Mammalia* 48:53–58.

Renquist, D., and Judge, F. 1985. Use of nylon balls as behavioral modifier for caged primates. *Lab. Primate Newsl.* 24 (4): 4.

Rhine, R. J., Norton, G. W., Wynn, G. M., and Wayne, R. D. 1985. Weaning of free-ranging infant baboons *(Papio cynocephalus)* as indicated by one-zero and instantaneous sampling of feeding. *Int. J. Primatol.* 6:491–99.

Richter, W. von. 1966. Untersuchungen über angeborene Verhaltensweisen des Schabrackentapirs *(Tapirus indicus)* und des Flachlandtapirs *(Tapirus terrestris). Zool. Beitr.* 12:67–159.

Roberts, M. S., Thompson, K. V., and Cranford, J. A. 1988. Reproduction and growth in the punare (*Thrichomys apereoides,* Rodentia: Echimyidae) of the Brazilian Caatinga with reference to the reproductive strategies of the Echimyidae. *J. Mammal.* 69: 542–51.

Rosenblatt, J. S. 1971. Suckling and home orientation in the kitten: A comparative developmental study. In *The biopsychology of development,* ed. E. Tobach, L. R. Aronson, and E. Shaw, 345–410. New York: Academic Press.

———. 1976. Stages in the early behavioural development of altricial young of selected species of non-primate mammals. In *Growing points in ethology,* ed. P. P. G. Bateson and R. A. Hinde, 345–83. New York: Cambridge University Press.

Sachs, B. D., and Harris, V. S. 1978. Sex differences and developmental changes in selected juvenile activities (play) of domestic lambs. *Anim. Behav.* 26:678–84.

Sade, D. S. 1973. An ethogram for rhesus monkeys. I. Antithetical contrasts in posture and movement. *Am. J. Phys. Anthropol.* 38: 537–42.

Sammarco, P. 1981. Great ape keeping at Lincoln Park Zoo. *Animal Keepers' Forum* 8:323–25.

Sanders, L. 1987. And how hot was it? *Animal Keepers' Forum* 14:345.

Schaller, G. B. 1963. *The mountain gorilla.* Chicago: University of Chicago Press.

———. 1972. *The Serengeti lion.* Chicago: University of Chicago Press.

Schoknecht, P. A. 1984. Growth and teat ownership in a litter of binturongs. *Zoo Biol.* 3:273–77.

Seyfarth, R. M. 1977. A model of social grooming among adult female monkeys. *J. Theor. Biol.* 65:671–98.

Seyfarth, R. M., and Cheney, D. L. 1984. Grooming, alliances, and reciprocal altruism in vervet monkeys. *Nature* 308:541–43.

Seyfarth, R. M., Cheney, D. L., and Hinde, R. A. 1978. Some principles relating social interactions and social structure among primates. *Recent Adv. Primatol.* 1:39–54.

Shoemaker, A. H. 1978. Observations on howler monkeys, *Alouatta caraya,* in captivity. *Der Zoologische Garten* 48:225–34.

Smith, P. K. 1982. Does play matter? Functional and evolutionary aspects of animal and human play. *Behav. Brain Sci.* 5:139–84.

Steiner, A. L. 1971. Play activity of Columbian ground squirrels. *Z. Tierpsychol.* 28:247–61.

Stevenson, M. F., and Poole, T. B. 1982. Playful interactions in family groups of the common marmoset *(Callithrix jacchus jacchus). Anim. Behav.* 30:886–900.

Struhsaker, T. T. 1967. *Behavior of vervet monkeys* (Cercopithecus aethiops). University of California Publications in Zoology, no. 82.

Sussman, R. W. 1977. Socialization, social structure, and ecology of two sympatric species of *Lemur.* In *Primate bio-social development,* ed. S. Chevalier-Skolnikoff and F. E. Poirier, 515–28. New York: Garland.

Symons, D. 1978. *Play and aggression: A study of rhesus monkeys.* New York: Columbia University Press.

Teicher, M. H., and Blass, E. M. 1976. Suckling in newborn rats: Elimination by nipple lavage, reinstated by pup saliva. *Science* 193:422–25.

———. 1977. First suckling response of the newborn albino rat: The role of olfaction and amniotic fluid. *Science* 198:635–38.

Tener, J. S. 1965. *Muskoxen in Canada: A biological and taxonomic review.* Monograph Series of the Canadian Wildlife Service, no. 2.

Thommen, D. R. 1982. Zur sozialentwicklung der Javaneraffen *(Macaca fascicularis)* wahrend der ersten drei lebensmonate. Ph.D. thesis, Basel University.

Thompson, K. V. 1985. Social play in the punaré *(Thrichomys apereoides):* A test of play function hypotheses. M.S. thesis, Virginia Polytechnic Institute and State University.

———. 1992. Reproductive competition, birth synchrony, and behavioral development in the sable antelope, *Hippotragus niger.* Ph.D. thesis, University of Maryland.

Thompson, V. D. 1986. Parturition and related behavior in the Queensland koala, *Phascolarctos cinereus,* at San Diego Zoo. *Int. Zoo Yrbk.* 26:217–22.

Trivers, R. L. 1974. Parent-offspring conflict. *Am. Zool.* 14:249–64.

———. 1985. *Social evolution.* Santa Cruz, Calif.: Benjamin Cummings.

Vaughan, T. A. 1978. *Mammalogy.* 2d ed. Philadelphia: Saunders College Publishing.

Vaughan, T. A., and Vaughan, R. P. 1987. Parental behavior in the African yellow-winged bat *(Lavia frons). J. Mammal.* 68:217–23.

Vincent, L. E., and Bekoff, M. 1978. Quantitative analyses of the ontogeny of predatory behaviour in coyotes, *Canis latrans. Anim. Behav.* 26:225–31.

Vogt, J. L., Carlson, H., and Menzel, E. 1978. Social behavior of a marmoset *(Saguinus fuscicollis)* group. I. Parental care and infant development. *Primates* 19:715–26.

Walters, R. H., and Parke, R. D. 1965. The role of distance receptors in the development of social responsiveness. *Adv. Child Dev. Behav.* 2:59–96.

Walther, F. 1962. Über ein Speil bei *Okapia johnstoni. Z. Säugetierk.* 27:245–51.

———. 1965. Verhaltensstudien an der Grantgazelle (*Gazella granti,* Brooke, 1872) im Ngorongoro-Krater. *Z. Tierpsychol.* 22:167–208.

West, M. 1974. Social play in the domestic cat. *Am. Zool.* 14:427–36.

White, L. E., and Hinde, R. A. 1975. Some factors influencing mother-infant relations in rhesus monkeys. *Anim. Behav.* 23:527–42.

Whitworth, M. R. 1984. Maternal care and behavioural development in pikas, *Ochotona princeps. Anim. Behav.* 32:743–52.

Wilson, S. 1973. The development of social behaviour in the vole *(Microtus agrestis). Zool. J. Linn. Soc.* 52:45–62.

Wilson, S. 1982. Contact-promoting behavior, social development, and relationship with parents in sibling juvenile degus *(Octodon degus). Dev. Psychobiol.* 15:257–68.

Wilson, S., and Kleiman, D. 1974. Eliciting play: A comparative study. *Am. Zool.* 14:331–70.

Winter, P., Ploog, D. W., and Latta, J. 1966. Vocal repertoire of the squirrel monkey *(Saimiri sciureus),* its analysis and significance. *Exp. Brain Res.* 1:359–84.

Zucker, E. L., Mitchell, G., and Maple, T. 1978. Adult male-offspring play interactions within a captive group of orangutans *(Pongo pygmaeus). Primates* 19:379–84.

35

Aspects of the Ecology and Psychology of Feeding and Foraging

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In nature, the lives of most mammals are dominated by a never-ending quest for food, resulting in strong selective pressures to maximize the efficiency with which they locate, subdue, or process food. These selective pressures have led to a host of morphological and physiological adaptations for feeding, from dentition and the size and shape of the tongue to the kinds of digestive enzymes produced and the structure and length of the digestive tract (Ricklefs 1979; Eisenberg 1981). The need to obtain food has led to a number of behavioral adaptations as well, which make use of various sensory mechanisms to identify edible plants or animals, spatial abilities to search efficiently for food, stalking behaviors, and even social cooperation to bring down very large prey. This chapter presents some of the basic concepts of the ecology and psychology of feeding in mammals and relates these to the management of mammals in captivity.

THE TYPE OF DIET CONSUMED

The diet of any animal species can be characterized by two related components: (1) the type of food selected and (2) the variety of foods consumed. Animals that eat only plants or their seeds and fruits are called herbivores, while animals that prey on other animals are called carnivores. Omnivores consume both plant and animal material. Still finer distinctions are sometimes made with regard to dietary type. For example, herbivores can be further broken down into folivores (leaf eaters), granivores (seed eaters), and frugivores (fruit eaters). But the utility of these distinctions is limited, since many mammals consume a combination of foodstuffs. This brings us to the second major component of diet: dietary breadth.

Animals that consume only one or a very few kinds of food are known as specialists. Classic examples of mammalian specialists include the giant panda, *Ailuropoda melanoleuca,* which feeds exclusively on bamboo; the koala, *Phascolarctos cinereus,* which eats only eucalyptus leaves; and the giant anteater, *Myrmecophaga tridactyla,* whose name bespeaks its rather limited diet. Specialists obtain the nutrients necessary for growth and reproduction from a very narrow range of foods. The foraging challenge facing specialists is to locate sufficient amounts of the appropriate material to sustain them. Their recognition of food is usually innate (Rozin 1976; Rozin and Schulkin 1990).

The captive management of extreme specialists can be very difficult. Regional populations of koalas, for example, are adapted to different species of eucalyptus leaves (Chinery 1992). Moreover, providing the mainstay of the specialist's diet may not be sufficient to ensure its good health. In nature, a specialist may obtain necessary nutrients from sources other than its primary food. For example, some mammals may occasionally consume soil or lick or chew mineral deposits. Very little is known about the nutrient requirements of specialists and how those requirements are met by their limited diets. Finally, temporal variation in the abundance of key food species in the specialist's native habitat may serve as a cue for reproduction. The cultivated diets fed to zoo animals may obscure these cues.

Generalists are at the opposite end of the dietary spectrum, choosing to feed on a variety of plants or animals. Since generalists consume a wide range of substances, it is unlikely that they innately recognize appropriate foods; rather, they rely on learning and experience (Rozin 1976; Rozin and Schulkin 1990). In addition, from the smorgasbord of edible substances in their environment, generalists must select a diet that is nutritionally well balanced.

Many of the mammals commonly exhibited in zoos are generalists, including bears, canids, and a host of primates. But few species rival the Norway rat, *Rattus norvegicus,* in willingness to eat almost anything. The extreme breadth of the rat's diet has endowed it with great versatility and is largely responsible for its current worldwide distribution.

The ability of rats to learn quickly to discriminate between edible and inedible substances has been the subject of considerable research, which is discussed below.

NEOPHOBIA AND FOOD AVOIDANCE

Few plants or animals passively accept their role as food for other organisms. One defense against predation that has evolved in a number of plants is the production or concentration of toxic substances known as secondary compounds (Feeney 1975; Freeland and Janzen 1974). Organisms protected by poisons or secondary compounds are generally avoided by potential consumers; however, many animals must learn to avoid these harmful species (Brower 1969).

Many animals faced with a new food are extremely suspicious of it and may avoid it for long periods of time. When they finally do ingest it, they take a very small amount. This wary response to novel foods, referred to as neophobia, has been observed in a variety of mammals and birds (Rozin 1976; Rozin and Schulkin 1990). Neophobic behavior is clearly adaptive. If the novel food turns out to be toxic, the mild effects of a low dose of poison will probably not be fatal, but the resulting discomfort will indicate that the food should be avoided in the future. Pairing of the discomfort with a clear visual cue (e.g., bright red coloration) or chemosensory cue (e.g., bitter taste) makes the learning that much faster. The readiness of animals to generalize their bad experience with one species to others that are similar in appearance has not gone unnoticed by natural selection. A multitude of edible species avoid being eaten by mimicking the appearance and behavior of distasteful species found in the same environment (Wickler 1968).

Classic studies of neophobia and poison avoidance were first conducted on wild rats by Richter (1953), Rzoska (1953), and Garcia et al. (1966). The rats were typically offered a flavored solution (e.g., vanilla) and allowed to drink it. Shortly thereafter, some of the rats were poisoned, either by exposure to x-rays or injection with lithium chloride. The rats that had been poisoned subsequently refused to drink the flavored solution when it was offered again. Surprisingly, these rats learned to associate the novel food flavor with negative consequences (i.e., the nausea induced by poisoning) after only a single pairing. Moreover, the rats learned this association even if several hours had passed between ingestion and poisoning. Subsequent studies demonstrated that wild rats are also able to distinguish between familiar and unfamiliar foods. If a rat consumes both a familiar and a novel food and then becomes sick, it will later avoid only the novel food (Shettleworth 1972).

Large generalist herbivores do not appear to possess the specialized food aversion learning mechanisms identified in the omnivorous rat. In studies of domestic cattle, sheep, ponies, and goats, Zahorik and Houpt (1981) found that although these species were able to form aversions to novel foods eaten as discrete meals when followed immediately by poisoning, they failed to learn the food aversion if there was a long delay (30 minutes or more) between ingestion and poisoning. The latter condition more accurately duplicates the situation faced by grazing animals in the wild, where they are more likely to encounter various slow-acting poisons (Freeland and Janzen 1974). Nonselective grazers such as the African buffalo, *Syncerus caffer,* or Burchell's zebra, *Equus burchellii,* are particularly unlikely to evolve food avoidance mechanisms since they consume a variety of plant species within an 8–12-hour feeding period (Beekman and Prins 1989). This feeding pattern makes specific associations between a particular plant and its toxic consequences difficult. Data on plant toxin aversion by zoo herbivores are lacking. Nevertheless, toxic ornamental plants should not be used in the vicinity of large herbivore enclosures.

INTER- AND INTRASPECIFIC DIFFERENCES IN NEOPHOBIA

Recent experiments suggest that the degree of neophobia can vary, even among closely related species. Greenberg (1984) studied the wintering ecology of two insectivorous tropical migrant birds in the lowland forests of Panama. He found that the bay-breasted warbler, *Dendroica castanea,* was more of a generalist and opportunist in its foraging behavior than the chestnut-sided warbler, *D. pennsylvanica.* In laboratory studies with immature animals of both species, he found that the chestnut-sided warbler was less willing to feed in a range of unfamiliar microhabitats than the bay-breasted warbler. His results indicate that young animals respond to novel feeding situations in ways that are appropriate to the feeding ecology of their species—that is, generalists are less neophobic than specialists.

Even within a species, there are clear differences in the degree of neophobia exhibited by individuals. Some animals are much more willing to try novel foods than others. The development of neophobia and the establishment of subsequent diet preferences has been shown to be mediated by early feeding experiences. Studies of Japanese macaque, *Macaca fuscata,* troops indicate that the acquisition of food preferences by juveniles results from the young's habit of ingesting scraps dropped by their mothers (Kawamura 1959). Social transmission of diet preference has also been reported in chacma baboons, *Papio ursinus,* mantled howler monkeys, *Alouatta palliata,* and meerkats, *Suricata suricatta* (reviewed in Galef 1976). Galef and Henderson (1972) have also shown that the diet of mother rats influences the preferences found in their offspring through gustatory cues incorporated into the flavor of the mother's milk.

The acquisition and persistence of early dietary preferences can have important consequences for the management of captive mammals (see part 2, Nutrition, this volume). While all mammals need nutritious, well-balanced diets, the exposure of young animals to a wide variety of foods, particularly through the use of adults as role models, may ensure that later changes to an animal's diet, due to a change in suppliers or translocation to another facility, are readily accepted.

SELECTING A BALANCED DIET

It is not enough for a foraging mammal to learn to avoid harmful substances; the animal must also consume a sufficient range of foods to satisfy all of its quantitative nutrient requirements. Early work with captive rats suggested that these animals selected a nutritionally balanced diet when offered a choice of items containing various amounts of carbohydrates, fats, proteins, vitamins, and minerals (Richter 1955). Evidence that mammals other than rats select balanced diets is equivocal, although some field studies report correlations between preferred diets and soluble concentrations of carbohydrates, proteins, minerals, and vitamins (cf. Westoby 1974).

In earlier studies, Richter (1943) demonstrated that rats are capable of responding to certain nutritional deficiencies by selecting diets that correct the deficiencies. The term "specific hunger" was used to describe the animal's innate preference for foods that contained the deficient nutrient. Rats with an increased need for sodium due to a deficient diet or adrenalectomy consumed higher quantities of sodium-rich foods. Likewise, rats deficient in vitamin B_1 preferentially consumed thiamine-rich foods.

The typical paradigm for these studies involved raising an animal on a diet lacking some essential nutrient (sodium or thiamine). When signs of the deficiency appeared, the animal was offered a choice between the original diet and a new diet that contained the missing nutrient. Rozin (1976) has argued that the preference for the new diet is not mediated by an innate recognition that the diet contains the missing nutrient; rather, the preference for the new diet is a result of a learned aversion to the original diet (the one that caused the illness) and therefore may be explained by the rat's poison avoidance mechanism. The observation that rats will eat less and less of a nutritionally deficient diet if not offered an alternative, even to the point of starvation, is consistent with this view (Rozin 1967).

The extent to which Rozin's rat studies can provide clues to feeding or appetite problems in captive animals is uncertain, however. While some mammals may have specific appetites for specific nutrients, we have no evidence that captive mammals possess the nutritional wisdom necessary to select a balanced diet. Specific hungers (e.g., sodium: cf. Schulkin 1991) and specific receptors (e.g., polysaccharide: cf. Rozin and Schulkin 1990) are known and help to explain food selection by some animals. However, the specific mechanisms that drive nutrient regulation are complex and are beyond the scope of this chapter.

BALANCING THE GOOD AND THE EVIL

In choosing an appropriate diet from the vast array of potential foods available in nature, certain mammalian species do not completely avoid potentially toxic species. In fact, the ecological literature is replete with examples of wild mammals that consume plant material known to contain toxic secondary compounds. Animals are able to survive on such diets only if they are able to detoxify these substances in the digestive tract, liver, or kidneys. But the need to detoxify may limit the amount of material that can be eaten at one time. It has been proposed that the range of plants typically consumed by mammalian herbivores is not a consequence of nutritional wisdom due to specific nutrient needs, but rather stems from their need to avoid damaging concentrations of any one particular toxin (Freeland and Janzen 1974).

A number of field studies have confirmed the importance of secondary plant compounds in the food selection of free-ranging primates. Oates, Swain, and Zantouske (1977) demonstrated that concentrations of tannin and alkaloids in leaves influenced the feeding behavior of black-and-white colobus monkeys, *Colobus guereza.* McKey et al. (1978) showed that secondary plant compounds affected black colobus, *C. satanas,* feeding strategies, while Glander (1981) found that mantled howler monkeys selected a diet that maximized their intake of total protein and water but minimized their intake of tannin and crude fiber.

Geophagy, or the ingestion of soil, has been observed in a variety of nonhuman primates. One explanation for this behavior is that certain soils contain compounds that help in the detoxification of secondary plant compounds (Hladik 1978; Oates 1978). A study by Gurian, O'Neill, and Price (1992) on free-ranging rhesus macaques, *Macaca mulatta,* in a large outdoor enclosure lends support to this view. The authors report that monkeys who were observed ingesting soil ate more of the vegetation growing within the enclosure than did non–soil consumers. Moreover, those monkeys who consumed the two vegetation types highest in tannin concentration—plantain leaves and yarrow roots—were all soil consumers. Previous studies have shown that kaolin, the active ingredient in Kaopectate, is found in clay soils and acts to neutralize toxins in the diet (Vermeer 1985).

In general, herbivorous mammals select from a broad spectrum of available foods. The bulk of the diet may be composed of a small subset of plants that satisfy the immediate caloric needs of the animal, while the remaining species consumed presumably satisfy other nutritional requirements (Belovsky 1978; Milton 1979; Robbins 1993).

INTRASPECIFIC DIFFERENCES IN DIET AND FORAGING BEHAVIOR

A number of field studies on primates report significant differences in the diet and foraging patterns of males and females (Clutton-Brock 1974; Gautier-Hion 1980; Pollock 1977; Rodman 1977; Waser 1977) or adults and juveniles (Van Schaik and Van Noordwijk 1986). Various explanations have been proposed to account for these differences, including sexual dimorphism, social dominance, and the changing nutritional needs of growing youngsters or reproductive females. Each of these explanations has received some empirical support, but several studies suggest that dominance interactions are primarily responsible for the observed differences in diet and foraging patterns within a species (Barton and Whiten 1993; Janson 1985; Wrangham and Waterman 1981). For example, Harrison (1983) found substantial differences between the diets of adult male and female green monkeys, *Cercopithecus sabaeus.* These differences were due to the competitive ability of males to dominate first-choice foods (fruits and flowers) as well as the tendency of lactating females to spend more time feeding on foods rich in protein (foliage, herbs, and grasses).

Social interaction also influences food selection in some species, particularly in opportunistic species with patchy or unpredictable food resources (Lefebvre and Palameta 1988; Caraco and Giraldeau 1991). While much work in this area has been done with honeybees, Galef (1988), in a series of studies, has demonstrated that foraging efficiency in Norway rats is enhanced by social interaction and exchange of olfactory signals.

Zoo managers typically attempt to minimize feeding competition in primates by chopping foods into very small pieces so that dominant animals cannot control all of the preferred food items. Yet Smith, Lindburg, and Vehrencamp (1989) report that this practice does not prevent dominant individuals from hoarding preferred foods. In their study, ten captive lion-tailed macaques, *Macaca silenus,* were presented with fruits and vegetables in either whole or chopped form. The authors found that the dietary diversity of the group was actually higher when foods were presented whole rather than chopped. In this study, the fruits and vegetables were scattered over a bare concrete floor. An alternative way to equalize access to preferred foods is to distribute the diet over a large three-dimensional area, preferably hiding the items in a variety of nooks and crannies within the enclosure.

SPATIAL DISTRIBUTION OF FOOD

Milton (1981) has suggested that the cognitive abilities of a species may be related to the spatial distribution or patchiness of its main food source. She examined differences in brain size and mental abilities between the red spider monkey, *Ateles geoffroyi,* and the mantled howler monkey, both of which live in the tropical forests of central Panama. The more frugivorous spider monkey was found to possess superior cognitive abilities and a larger brain. Milton argued that this was due to the fact that the spider monkey requires greater spatial memory to keep track of the changing resources within its enormous home range than does the more folivorous howler monkey.

The spatial distribution of food in a species' natural habitat influences its preferred strategies for foraging in captivity as well. Roberts and Cunningham (1986) found that adult western tarsiers, *Tarsius bancanus,* are extremely reluctant to hunt for insects on the floor of their enclosure. This foraging preference is consistent with the vertical stratification of their orthopteran prey in nature. It is important for zoo managers to consider the natural foraging behavior of a species when deciding how to present the diet in a captive setting.

CONCLUDING REMARKS

Much attention is now focused on the optimum foraging strategies of animals. This is a relatively new field that embraces the disciplines of psychology and behavioral ecology (Shettleworth 1984). A species' natural mechanisms for food recognition, capture, and processing will influence how it will forage in captivity. Many natural foraging behaviors, however, will not be expressed in the captive environment due to the physical form and spatial arrangement of the zoo diet. The stalking behaviors of carnivores, for example, will not be elicited by a food pan heaped with feline diet. Maintaining such behaviors in captivity may require the occasional presentation of novel foods, live prey, or the use of appropriate enrichment devices (see Carlstead, chap. 31, this volume).

The concentration and predictability of zoo diets is also quite unlike what is found in the natural world. Edible substances are usually patchily distributed in the environment, and require extensive time to collect and consume in sufficient amounts. Moreover, most wild mammals experience great seasonal variation in the composition of their diets as populations of major prey species fluctuate and plants go through their annual cycles of leaf, fruit, or seed production (Eagle and Pelton 1983; Karasov 1985; MacCracken and Hansen 1987).

The dietary preferences exhibited by species in captivity may be different from those observed in the wild. The time or energy costs involved in handling certain food items, such as nuts with heavy shells, are often removed in the processed diets offered in captivity. This practice can result in a higher ranking for such "difficult" items in captive studies of food choice. Species in the wild may also experience considerable interspecific competition, leading to a high degree of niche separation and dietary specialization. In zoos, even in mixed-species exhibits, major ecological competitors are rarely housed together. The absence of competitors will tend to broaden the diet choices exhibited by zoo animals. Therefore, a thorough understanding of both the ecology and psychology of wild feeding behaviors is critical if the results of captive studies are to be fully understood.

REFERENCES

Barton, R. A., and Whiten, A. 1993. Feeding competition among female olive baboons, *Papio anubis. Anim. Behav.*46:777–89.

Beekman, J. H., and Prins, H. H. T. 1989. Feeding strategies of sedentary large herbivores in East Africa with emphasis on the African buffalo, *Syncerus caffer. Afr. J. Ecol.* 27:129–47.

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: The moose. *Theor. Popul. Biol.* 14:105–34.

Brower, L. P. 1969. Ecological chemistry. *Sci. Am.* 220:22–29.

Caraco, T., and Giraldeau, L.-A. 1991. Social foraging: Producing and scrounging in a stochastic environment. *J. Theor. Biol.* 153: 559–83.

Chinery, M., ed. 1992. *Illustrated encyclopedia of animals.* New York: Kingfisher Books.

Clutton-Brock, T. H. 1974. Activity patterns of red colobus *(Colobus badius tephrosceles). Folia Primatol.* 21:161–87.

Eagle, T. C ., and Pelton, M. R. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. *International Conference on Bear Research and Management,* 5: 94–101.

Eisenberg, J. F. 1981. *The mammalian radiations: An analysis of trends in evolution, adaptation, and behavior.* Chicago: University of Chicago Press.

Feeney, P. P. 1975. Biochemical evolution between plants and their insect herbivores. In *Coevolution of animals and plants,* ed. L. E. Gilbert and P. H. Raven. Austin: University of Texas Press.

Freeland, W. J., and Janzen, D. H. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.* 108:269–89.

Galef, B. G. 1976. Social transmission of acquired behavior: A discussion of tradition and social learning in vertebrates. *Adv. Stud. Behav.* 6:77–100.

———. 1988. Communication of information concerning distant diets in a social, central place foraging species: *Rattus norvegicus.* In *Social learning: Psychological and biological perspectives,* ed. T. R. Zentall and B. G. Galef, 119–39. Hillsdale, N.J.: Lawrence Erlbaum Associates.

Galef, B. G., and Henderson, P. W. 1972. Mother's milk: A determinant of the feeding preferences of weaning rat pups. *J. Comp. Physiol. Psychol.* 78:213–19.

Garcia, J., Ervin, F. R., and Koelling, R. A. 1966. Learning with prolonged delay of reinforcement. *Psychonomic Sci.* 5:121–22.

Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of Ceropithecus monkeys. *J. Anim. Ecol.* 49:237–69.

Glander, K. E. 1981. Feeding patterns in mantled howler monkeys. In *Foraging behavior: Ecological, ethological and psychological approaches,* ed. A. C. Kamil and T. D. Sargent, 231–57. New York: Garland Press.

Greenberg, R. 1984. Differences in feeding neophobia in the tropical migrant wood warblers, *Dendroica castanea* and *D. pennsylvanica. Comp. Psychol.* 98:131–36.

Gurian, E., O'Neill, P. L., and Price, C. S. 1992. Geophagy and its relation to tannin ingestion in rhesus macaques *(Macaca mulatta). AAZPA Regional Conference Proceedings,* 152–59. Wheeling, W.Va.: American Association of Zoological Parks and Aquariums.

Harrison, M. J. S. 1983. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus. Anim. Behav.* 31:969–77.

Hladik, C. M. 1978. Adaptive strategies of primates in relation to leaf eating. In *The ecology of arboreal folivores,* ed. G. G. Montgomery, 373–95. Washington, D.C.: Smithsonian Institution Press.

Janson, C. H. 1985. Aggressive competition and food consumption in the brown capuchin monkey *(Cebus apella). Behav. Ecol. Sociobiol.* 18:125–38.

Karasov, W. H. 1985. Nutrient constraints in the feeding ecology of an omnivore in a seasonal environment. *Oecologia* 66: 280–90.

Kawamura, S. 1959. The process of sub-culture propagation among Japanese macaques. *Primates* 2:43–60.

Lefebvre, L., and Palameta, B. 1988. Mechanisms, ecology, and population diffusion of socially learned food-finding behavior in feral pigeons. In *Social learning: Psychological and biological perspectives,* ed. T. R. Zentall and B. G. Galef, 141–64. Hillsdale, N.J.: Lawrence Erlbaum Associates.

MacCracken, J. G., and Hansen, R. M. 1987. Coyote feeding strategies in southeastern Idaho: Optimal foraging by an opportunisitic predator? *J. Wildl. Mgmt.* 51 (2): 278–85.

McKey, D., Waterman, P. G., Mbi, C. N., Gartlan, J. S., and Struhsaker, T. T. 1978. Phenolic content of vegetation in two African rainforests: Ecological implications. *Science* 202: 61–64.

Milton, K. 1979. Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *Am. Nat.* 114:362–78.

———. 1981. Distribution of tropical plant foods as an evolutionary stimulus to primate mental development. *Am. Anthropol.* 3: 534–48.

Oates, J. 1978. Water-plant and soil consumption by guereza monkeys *(Colobus guereza):* A relationship with minerals and toxins in the diet? *Biotropica* 10:241–53.

Oates, J. F., Swain, T., and Zantouske, J. 1977. Secondary compounds and food selection by colobus monkeys. *Biochem. Syst. Ecol.* 5:317–21.

Pollock, J. I. 1977. The ecology and sociology of feeding in *Indri indri.* In *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes,* ed. T. H. Clutton-Brock, 276–319. London: Academic Press.

Richter, C. P. 1943. Total self regulatory functions in animals and human beings. *Harvey Lect.* 38:63–103.

———. 1953. Experimentally produced reactions to food poisoning in wild and domesticated rats. *Ann. N.Y. Acad. Sci.* 56: 225–39.

———. 1955. Self-regulatory functions during gestation and lactation. *Trans Conf. Gestation,* 2d, Princeton, N.J., 11–93.

Ricklefs, R. E. 1979. *Ecology.* 2d ed. New York: Chiron Press.

Robbins, C. T. 1993. *Wildlife feeding and nutrition.* 2d ed. San Diego, Calif.: Academic Press.

Roberts, M., and Cunningham, B. 1986. Space and substrate use in captive Western tarsiers, *Tarsius bancanus. Int. J. Primatol.* 7: 113–30.

Rodman, P. S. 1977. Feeding behavior of orangutans of the Kutai Nature Reserve, East Kalimantan. In *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes,* ed. T. H. Clutton-Brock, 384–413. London: Academic Press.

Rozin, P. 1967. Specific aversions as a component of specific hungers. *J. Comp. Physiol. Psychol.* 64:237–42.

———. 1976. The selection of foods by rats, humans, and other animals. *Adv. Stud. Behav.* 6:21–76.

Rozin, P. N., and Schulkin, J. 1990. Food selection. In *Handbook of Behavioral Neurobiology,* vol. 10, *Neurobiology of food and fluid intake,* ed. E. M. Striker. New York: Plenum Press.

Rzoska, J. 1953. Bait shyness, a study in rat behavior. *Brit. J. Anim. Behav.* 1:128–35.

Schulkin, J. 1991. *Sodium hunger: The search for a salty taste.* Cambridge: Cambridge University Press.

Shettleworth, S. 1972. Constraints on learning. *Adv. Stud. Behav.* 4:1–68.

———. 1984. Learning and behavioral ecology. In *Behavioral ecology: An evolutionary approach,* 2d ed., ed. J. R. Krebs and N. B. Davies, 170–94. Oxford: Blackwell Scientific.

Smith, A., Lindburg, D. G., and Vehrencamp, S. 1989. Effect of food preparation on feeding behavior of lion-tailed macaques. *Zoo Biol.* 8:57–65.

Van Schaik, C. P., and Van Noordwijk, M. A. 1986. The hidden costs of sociality: Intra-group variation in feeding strategies in Sumatran long-tailed macaques *(Macaca fuscata). Behaviour* 99:296–315.

Vermeer, D. E. 1985. Nigerian geophagical clay, traditional antidiarrheal pharmaceutical. *Science* 227:634–36.

Waser, P. 1977. Feeding, ranging, and group size in the mangabey *Cercocebus albigena.* In *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes,* ed. T. H. Clutton-Brock, 183–222. London: Academic Press.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. *Am. Nat.* 108:290–304.

Wickler, W. 1968. *Mimicry in plants and animals.* London: World University Library.

Wrangham, R. W., and Waterman, P. G. 1981. Feeding behavior of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea* with special reference to reproductive strategies and tannin production. *J. Anim. Ecol.* 50:715–31.

Zahorik, D. M., and Houpt, K. A. 1981. Species differences in feeding strategies, food hazards, and the ability to learn food aversions. In *Foraging behavior: Ecological, ethological and psychological approaches,* ed. A. C. Kamil and T. D. Sargent, 289–310. New York: Garland Press.