II. SUBORDER: PROSIMII
Family: Lemuridae (Lemurs)
Indriidae (Indris)
— 4 —
Maintenance of Primates in Captivity for Research: The Need for Naturalistic Environments

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ABSTRACT

The physiology and behavior of nonhuman primates comprise biological systems that are coadapted to particular physical and social environments that are normally present throughout development. Maintenance of wild-caught and laboratory-born primates in small, individual cages precludes social interaction and other experiences likely to be essential to regulation of physiology and behavior in these animals. Just as inbreeding can destroy much genetically-controlled developmental homeostasis, so maintaining intrinsically gregarious animals like primates in isolate caging is likely to engender idiosyncratic physiologico-behavioral response patterns. The validity of biomedical or behavioral research conducted with such subjects remains indeterminate without appropriate control procedures, viz., comparisons of individually-caged subjects with animals living in species-appropriate social groups and environments. Because the Duke University Primate Center is dedicated to the breeding and conservation of prosimian primates, all colony members have always been housed in social groups. For some lemur species, however, even housing animals socially in large indoor rooms outfitted with naturalistic substrata has proven inadequate to promote normative behavior. For sifakas (*Propithecus verreauxi*), providing them with outdoor living space produced dramatic improvements in activity patterns and reproductive effort. The endpoint of our husbandry program for lemurs is placement of social groups in large natural habitat enclosures to prepare them for the possibility of reintroduction to protected natural ranges. With the completion of our newest enclosures, the Duke Primate Center has provided

nearly 100 lemurs, members of seven endangered species, more than 11 hectares (28 acres) of forest in which to acquire skills in climbing and traveling in trees, foraging, and avoiding predators. Simultaneously, the welfare of individual colony members remains our top priority while the most advanced research on the behavior and reproductive biology of understudied, endangered primates is facilitated. Such research should ultimately promote future reintroduction efforts. The husbandry and research done at the Duke Primate Center, therefore, are humane and valuable for the primates involved, for both the individuals and their populations.

PRIMATE NATURAL HISTORY AND BIOMEDICAL RESEARCH

In designing facilities for maintenance of nonhuman primates in captivity, it is essential to realize that primates are social animals. Naturally-occuring primate social groups frequently number between 50 and 100 members (Altmann & Altmann 1970; Kummer 1968; Rowell 1972), and some number well over 100 (Baldwin & Baldwin 1971; Poirier & Hu 1983). Thirty-nine of the 54 primate genera (Richard 1985), or 70% of extant forms, coalesce into social groups that include two or more unrelated adults and their infant and juvenile offspring. Even primates formerly thought to lead "solitary" lives, like orang-utans (*Pongo pygmaeus*) and bushbabies (*Galago* and *Euoticus* spp.), are now known to be genuinely social (see, e.g., Clark 1978; Rijksen 1978; Harcourt & Nash 1986). Much remains to be learned about the structure of primate societies and the nature of primate social interaction through study of these species.

The primary adaptations of primates have evolved in environments that include complex social interactions within groups and populations of broadly stable composition. In virtually every species studied, maturing individuals develop strong, long-term affinitive relations with their mothers, siblings, and unrelated conspecifics between birth and adulthood. In most Old World monkeys, for example, infants are nurtured intimately by their mothers for about a year. In the matrix of the social group, infants explore and play; their mothers retrieve them from occasional "mistakes" they make in interaction with both social and physical features of their environment. Hours of sleeping and nursing are accompanied daily by maternal grooming. Through observation during infancy, youngsters learn their family's social status (Berman 1980 1982ab; Altmann 1980; Pereira 1988b), what and how to eat (Watts 1985; Whitehead 1986; Pereira 1988a), and how to detect and respond to predators. For two to four years after weaning and before puberty, juveniles further develop relations with their mothers, siblings, and peers, and initiate important relationships with unrelated group members (Pereira & Altmann 1985). Affinitive interactions, including greetings, grooming, social play, and sleeping associations, balance the agonistic interactions and competition that accompany group living (Judge 1982;

Smuts 1985; de Waal 1986). For primates, normative behavioral development is a life-long process that depends on continuous input from myriad ecological and social stimuli (Pereira & Altmann 1985).

Consider now that the vast majority of biomedical research using primates evaluates data gathered from individuals confined in tiny, barren, isolated cages. Subjects are taken from their social groups in the wild as immatures or adults while others are born into laboratory cages. Laboratory-born primates usually begin life with their mothers in small isolation cages, and are separated from them before the normal age of weaning (cf Altmann 1980; Berman 1982ab). They spend their early juvenile years either alone or with a small group of peers in other barren cages, and then spend the rest of their lives in a cage less than one meter tall that offers about three-quarters of a square meter of floor space. These are the current space recommendations in the NIH *Guide for the Care and Use of Laboratory Animals* (USDHHS 1985) for proper management of baboons in laboratories.

Under such conditions, nonhuman primates cannot express normal patterns of physiology or behavior. Indeed, behavioral biologists would predict that subjecting primates to these conditions must produce multifarious aberrancies in both systems. This prediction derives from the axiomatic premise that normal primate physiology and behavior are systems coadapted to particular physical habitats and social environments invariably present throughout natural development (Figure 1). A primate deprived of regulatory environmental stimuli should thus be expected to exhibit atypical features in its baseline and responsive physiology and behavior. A critical conclusion emerges from this argument that must be addressed both by the scientific community and by society: valid biomedical research cannot be conducted on primates or other social species in existing laboratory environments. Because we must suspect the normalcy of physiologico-behavioral responses in any social organism maintained in restrictive, abnormal environments, the validity, and thus value, of any research based on such subjects is questionable. Fox (1986a) cogently expands this argument, reviewing generalities and heuristic examples for many species commonly used in animal laboratories.

The 1985 NIH *Guide* states that good biomedical research must consider the effects of environmental factors on the wellbeing and biologic responses of research animals. The *Guide* also warns, however, that proper management includes genetic and environmental control to minimize variations in animals' responses to experimental regimens. Unfortunately, this principle has traditionally been misinterpreted to mean that extensive inbreeding and minimal, sterile, isolate housing will minimize any baseline variance in physiology and behavior among research subjects. The presumption concerning inbreeding and variability is, in many cases, demonstrably false: phenotypic variance in laboratory rodents, for example, often increases with degree of inbreeding (Russell & Burch 1959; Lane-Petter & Pearson 1971; Festing 1979). Variability in the physiology and behavior of social mammals probably also increases with the degree of isolation and restriction imposed by their captive environments. Just as inbreeding destroys much genetically-controlled developmental homeostasis, so must maintenance of intrinsically gregarious animals in small, isolate cages generate a multitude of idiosyncratic physiologico-behavioral response patterns by precluding essential regulatory experience.

A vast literature exists describing effects of housing style and group composition on the physiological functioning of laboratory animals. Over the past 30 to 40 years, research has related differences in captive social environments to differential development of brains, musculoskeletal anatomy, neuroendocrine systems, immunological systems, behavior, and reproductive performance (Fox 1986a reviews much important literature; see also the pertinent discussion by Fagen [1981] of related research). At the 1983 public hearing in Chicago preceding revision of the NIH *Guide*, Pereira and Altmann (1983) provided the Institute of Laboratory Animal Resources' (ILAR) Committee with a bibliography of 150 articles selected from this literature. Each article documented changes effected by social or other environmental factors on aggression, reproduction, infanticide, pituitary-adrenal or pituitary-gonadal function, resistance to chronic physical ailments or infectious disease or response to drugs or toxins in laboratory animals. The most surprising feature of the available literature reviews is the revelation that relationships between captive environments and physiologico-behavioral functioning have been virtually ignored for primates (see review in Nash & Chilton 1986). This has occurred despite primates' status as the most valuable animal models for biomedical research (but see Newell-Morris & Fahrenbruch 1985, for primatologists' criticism of Cercopithecinae and other primates as models for human biology).

In response to present concerns, the ILAR committee recommended that "when appropriate, group housing should be considered for communal animals" (USDHHS 1985, p. 12), but concluded that "there is little objective evidence for defining adequate care in relation to social environment. The data are limited and contradictory and lack sufficient substance to establish absolute recommendations" (p. 12). Other readers of the literature believe a more extensive response is needed to the current ratio of knowledge to ignorance regarding these issues (e.g., Pereira & Altmann 1983; Fox 1986a). Lack of uniformity in effects of housing on physiology and behavior detracts in no way from the import of that vast body of research. Features of biomedical laboratories and research methodology that destroy or thwart homeostatic mechanisms should be expected to *generate* variability, within and across species. Additional variability is to be expected in results emerging from different laboratory environments and from species that have evolved vastly different types of sociality and ranging. The degenerate responses often produced by chronic isolate caging even in animals that are less social than primates (see literature cited in Fagen 1981; Pereira & Altmann 1983; Fox 1986a) foretell likely severe effects on species that natu-

rally exhibit pronounced gregariousness and complex forms of social organization.

In the remainder of this chapter, we review recent research conducted at the Duke University Primate Center that illustrates the impact that housing style can have on primate behavior and physiology, and thus on the validity of research using captive primates. We highlight a study that revealed effects of indoor versus outdoor housing on the activity budgets and reproduction of our sifakas (Indriidae: *Propithecus verreauxi*). We conclude by discussing critical implications for researchers studying primates in more restrictive settings, and suggested guidelines for improved housing for primates maintained for biomedical and behavioral research.

The Duke University Primate Center

The Duke University Primate Center is dedicated to the breeding and conservation of prosimians and to training conservationists and researchers for work with these species. Prosimians comprise seven of the 14 Primate families: Lemuridae and Lepilemuridae (true lemurs), Cheirogaleidae (mouse and dwarf lemurs), Indriidae (indris, avahis, and sifakas), Daubentoniidae (aye-ayes), Lorisidae (lorises and galagos), and Tarsiidae (tarsiers). Extant lemuriform species (first five families mentioned above) are found only in Madagascar and all are considered endangered. Many are now seen only occasionally in their homeland (Jolly 1986; Pollock 1986a), and several are not in captivity anywhere other than at the Duke Primate Center (Tattersall 1982; Pollock 1986b). The Duke Primate Center has an unrivaled record of captive survival and breeding with several of the species most difficult to rear in captivity, and we now maintain over thirty prosimian taxa, including about 720 individuals. The real threat of extinction for several prosimian species over the next 10 to 15 years has led to international recognition of the Duke collection as a critical second line of defense against the prospect of extinction for prosimian primates (Tattersall 1982; Jolly 1986; Pollock 1986ab; Richard 1982).

Since the 1960's, the Duke Center has also been a focus of research into the behavior and reproductive biology of prosimians. Because Madagascar was virtually closed to outside researchers between 1972 and 1982, research on lemurs at Duke took on additional importance. Information on olfactory behavior, learning, mother-infant relations, reproductive biology, vocalizations, metabolic rates, development, and social behavior has come from research with the Duke colony (for recent work, see Foerg 1982; Hoffman & Foerg 1983; Glander & Rabin 1983; Izard & Rasmussen 1985; Macedonia & Taylor 1985; Rasmussen 1985 1986; Taylor & Sussman 1985; Ganzhorn 1986 1987; Izard & Simons 1986; Macedonia 1986 1987; Wright Izard & Simons 1986; Wright Toyama & Simons 1986; Pereira & Simons 1986; Cherry Izard & Simons 1987; Gebo 1987; Kappeler

1987ab; McNab & Wright 1987; Pollock & Mullin 1987; Pereira Klepper & Simons 1987; Rasmussen & Izard 1988; Haring in press; Pereira Seeligson & Macedonia in press).

At the Duke Primate Center, however, the survival and reproductive success of every colony member have always been of first concern. Consequently, all colony members have been housed under naturalistic conditions and no research procedures more invasive than withdrawal of blood samples and occasional biopsies have been allowed. Surrounding the main building are more than 50 outdoor runs or cages made of chain-link or lighter-weight fencing that enclose between 25 and 250 cubic meters of space and numerous branch substrata. Most runs have a top fence in lieu of a roof to allow the family group of lemurs to experience natural patterns of sunlight, wind, and rain. Each run also has one or more elevated boxes containing shielded heat lamps to provide refuge from the most severe North Carolina weather.

The lemurs in our outdoor runs provide a unique resource for comparative research on prosimian behavior and reproductive biology. We maintain several different social groups of each species, providing diverse opportunity for research within and across taxa that are together in one place only at the Duke Center. Social groups of many lemur species are also maintained in multi-hectare forest enclosures (see below; also Taylor & Sussman 1985; Ganzhorn 1986; Macedonia 1986; Pereira et al. 1987; Simons 1986; Glander in press; Pereira Seeligson & Macedonia in press). While most large-bodied lemurs are maintained outdoors, our small-bodied mouse and dwarf lemurs, tarsiers, lorises, and galagos are held in social groups inhabiting indoor rooms outfitted with naturalistic substrata a(Izard & Pereira 1987).

DUKE PROGRAM FOR CAPTIVE CONSERVATION OF SIFAKAS

Since the inception of the Duke University Primate Center (1966, and before, when the collection was maintained at Yale University), the Center has been the only institution outside Madagascar to maintain and breed sifakas, obtaining our first sifaka from Madagascar in 1960. Sifakas are large (4-6 kg), diurnal lemurs of which two species are recognized: *Propithecus diadema*, which inhabits Madagascar's eastern rain forests, and *P. verreauxi* (Figure 2), which survives in the island's remaining western deciduous forests and southern spiny forests (Tattersall 1982; Pollock 1986a; Jolly 1986). Like other indriid lemurs (*Indri indri* and *Avahi laniger*), the diet of wild sifaka consists primarily of leaves, although considerable quantities of fruit, flowers, and tree bark are also ingested (Richard, 1978).

Also like the other indriids, sifakas are endangered primates that have proven difficult to maintain in captivity. Until relatively recently, all attempts to sustain and breed indriids in captive settings have had poor

results. Because these lemurs exhibit specializations of the digestive tract for processing fibrous plant materials, it is possible that inappropriate diets have been responsible for the premature deaths of many captive individuals. A characteristic "wasting" syndrome, marked by progressive disinclination to eat, lethargy, and eventual death, has led to the abandonment of attempts to maintain three of the four species of Indriidae in captivity.

Beginning in the mid-1970s, mortality among Duke sifakas increased sharply, leaving the captive-born male as the colony's sole survivor. Because the sifakas population continues to dwindle in Madagascar, one of us (Simons), having taken over as Director of the Primate Center in 1978, established unique agreements with the Malagasy government, allowing the Center to obtain new sifakas in 1982 and again in 1984 and 1986. An intensive, stepwise program of husbandry was developed, designed to maintain high survivorship while gradually increasing the degree to which the colony's living conditions approximated natural environments. These measures were expected to improve activity patterns and breeding success.

At first, the sifakas were housed in large rooms (about 85 cu m). The amount of naturalistic substrata in these rooms, including tree trunks and branches, was increased to simulate more closely natural environments. Next, the sifaka diet was improved. An increased supply of mango leaves was obtained through a volunteer network in southwestern Florida and Miami. Later, we discovered that related lemurs (Lemuridae) readily consume leaves from a number of local plants, while rejecting plants that contain high levels of alkaloids (Glander & Rabin 1983; Ganzhorn 1986). Consequently, leaves from several local trees were added to the sifaka diet (see below). In 1985, additional changes in housing and diet led to radical improvements in the health, vigor, and reproduction of these animals.

Modifications of the Sifaka Diet

Because wild sifakas are known to eat mango leaves (E. Simons, personal observation), the Duke sifakas have been provisioned with mango leaves for a number of years. Preliminary nutritional analyses of mango leaves failed to reveal an unusual nutrient profile that might have allowed us rapidly to improve the composition of the sifaka diet (K. Glander, personal communication). In 1985, however, we began to introduce local North Carolina foliage to supplement the regular sifaka diet of mango leaves, cut fruit and vegetables, and monkey chow (Table 1; Haring, in press). Plants seen to be eaten by several lemurid species inhabiting two forest enclosures (Ganzhorn 1986) comprised the list of potential food species. Initially, only plant parts consumed by all lemurid species were offered to the sifakas. In addition to species preferences, seasonal preferences in the plant parts selected by our semi-free-ranging Lemuridae were followed in choosing local foliage for the sifakas.

At the onset of the program, two to three local plant foods were

introduced each week. All plant material was first rinsed with water. Then terminal branch parts with their leaves were inserted into plastic water containers secured to tree trunks in the sifaka rooms. If a food was accepted, it became a regular part of the daily sifaka diet. Plant species initially rejected were offered again periodically. Some plants were only sniffed or nibbled at first, but later eaten in sizable quantities. Foods repeatedly rejected were dropped from the diet. During the summer and fall of 1985, four or five of the accepted plant species were presented fresh daily along with mango leaves, fresh cut fruit, and chow. Beginning in the spring of 1986, the sifakas were fed three to five of the previously accepted plant parts plus two to four new species each week.

Fig. 1: Social environment to which behavior & physiology of ringtailed lemurs (*Lemur catta*) are coadapted. Young adult female in center carries her 3-mo-old son while being groomed by her juvenile sister. In front of her are two offspring of her adult sisters; to the left are two adolescent males: her cousin & nephew. Ringtailed lemurs are remarkably socially cohesive in comparison to ruffed lemurs (*Varecia variegata*) and chimpanzees (*Pan troglodytes*). (Photo by MEP.)

Table 1

Diet of Duke Sifakas Prior to 1985

Fruits	Vegetables	Other Foods
apple	broccoli	Science Chow
avocado	cabbage	hard-boiled egg
banana	carrot	cottage cheese
grape	cauliflower	mango leaf
mango	celery	sweetgum leaf
melon	corn	
orange	cucumber	
peach	garbanzo bean	
pear	lettuce	
pineapple	sweet potato	

Table 2 shows that five North Carolina plant species have become dietary staples for the Duke sifakas, with an additional five species eaten on a seasonal basis (Haring in press). We found that naive individuals more readily accepted novel plant species when in the company of colony members previously exposed to those species (also Whitehead 1986). Captive-born infants and newly-acquired wild-caught adults sniffed at length those plant species that were unfamiliar to them but consumed by others in their group. The naive animals also persistently smelled the hands and mouths of animals that had consumed the new foliage.

In addition to providing local foliage during its growing season, the DUPC has begun to freeze leaves during the season of their acceptance for winter provisioning. At present, it appears that leaves of most of the tree species used undergo freezing and thawing with little adverse effect on palatability (Haring in press).

Modification of Sifaka Housing Environments

Early in the summer of 1985, the first attempt began to house a sifaka group outdoors. Previously, only one individual was housed outdoors, due to concern over exposure of these rare animals to potentially dangerous pathogens. That project terminated when the subject in fact became ill. Continued low activity levels and sub-optimal reproduction in the Duke sifakas, however, demanded that outdoor environments be established. In June 1985, a group of sifakas (Group 3) was moved to a large outdoor cage directly adjacent to the main building. Behavioral data gathered from this

Figure 2. Adult sifaka (*Propithecus verreauxi coquereli*) feeding in a forest enclosure at the Duke University Primate Center. (Photograph by DMH.)

Table 2
Local North Carolina Plants Offered As Food to Duke Sifakas in 1985/1986

Species Accepted	Part/Level
American hornbeam (*Carpinus caroliniana*)	lv / *
mimosa (*Albizia julibrissin*)	fr,fl,lv/*
Eastern redbud (*Cercis canadensis*)	sd,fl,lv / *
winged sumac (*Rhus copallina*)	fl,lv/*
sweetgum (*Liquidambar styraciflua*)	bd,lv / *
beech (*Fagus grandifolia*)	lv / +
blackberry (*Rubus* sp.)	lv / +
crabapple (*Malus angustifolia*)	fr / +
red maple (*Acer rubrum*)	fr,fl,lv / +
rose (*Rosa multiflora*)	fl,lv / +
boxelder (*Acer negundo*)	lv / o
blackgum (*Nyssa sylvatica*)	fl,lv / o
kudzu (*Pueraria lobata*)	lv / o
loblolly pine (*Pinus taeda*)	lv / o
tulip poplar (*Liriodendron tulipifera*)	lv / o

Species Rejected	Part/Level
alder (*Alnus serrulata*)	fl,lv
white ash (*Fraxinus americana*)	lv
catalpa (*Catalpa speciosa*)	lv
dogwood (*Cornus florida*)	fl,lv
elm (*Ulnus americana*)	sd,fl,lv
grape (*Vitis rotundifolia*)	fr,lv
greenbriar (*Smilax* sp.)	lv
hickory (*Carya* sp.)	lv
holly (*Ilex opaca*)	lv
honeysuckle (*Lonicera japonica*)	fl,lv
mulberry (*Morus rubra*)	lv
persimmon (*Diospyros virginiana*)	fr,lv
river birch (*Betula nigra*)	lv
sourwood (*Oxydendrum arboreum*)	fl,lv
sycamore (*Platanus occidentalis*)	lv
trumpet vine (*Campsis radicans*)	lv
black willow (*Salix nigra*)	fl,lv

lv=leaves; fl=flowers; fr=fruits; sd=seeds; bd=buds
* eaten throughout growing season
\+ eaten only seasonally
o eaten by only a few individuals

group (Group 3) were compared to data previously gathered from the same group while it was housed indoors and to data taken concurrently from other indoor sifaka groups. We predicted that the experimental setting would stimulate activity, including feeding, and lead to improved health and reproductive effort. Table 3 lists the activities studied.

Analyses of activity budgets revealed significant increases for Group 3 in time spent locomoting, playing, and feeding (all $p < 0.05$; Fig. 3), and a significant decrease in time spent inactive ($p < 0.05$; Fig. 4), in comparison to the concurrent activity budgets of four indoor groups (Macedonia 1987 gives details of the statistical analyses). Examination of correlations between frequencies of outdoor activities and ambient temperature, time of day, and degree of cloud cover revealed no effects of these variables.

One variable that could have influenced activity in Group 3 was enclosure size. The outdoor cage this group lived in measured about 234 cu-m, roughly three times the volume of their former indoor rooms (82 cu-m). Therefore, an investigation was undertaken in 1986 that focused upon possible effects of enclosure size in stimulating activity in captive sifakas. One group (Group 4) was provided access to an outdoor extension of their quarters that was considerably smaller (about 60 cu-m) than their indoor room. Members of this group could move freely between indoor and outdoor chambers.

Comparison of Group 4's activity budgets in the novel indoor/outdoor environment with their activity budgets the previous year (indoors only) revealed significant increases in time spent locomoting ($p < 0.005$) and playing ($p < 0.05$; Fig. 5) and a significant decrease in time spent resting ($p < 0.005$; Fig. 4). Increases in time spent feeding approached significance ($p = 0.10$). Most important, we found that well over 90% of time was spent in the outdoor compartment, despite its smaller size. That the larger, indoor chamber was not preferred suggests that, in the previous studies, enclosure volume *per se* played little, if any, role in the observed changes in activity budgets. The results suggest either that sifakas prefer outdoor over indoor housing or new over old cage space. Continuing predominant use of outdoor space during warmer months by sifakas in indoor/outdoor quarters fail to support the novelty hypothesis. Members of Group 4 spent more than 75% of their time indoors feeding upon food placed indoors or resting near heat lamps. Also, during the winter and early spring of 1987, a female sifaka with a young infant appeared to prefer her indoor room. Pereira et al. (1987) discuss the importance of behavioral thermoregulation for prosimian infants.

Table 3

Activities Quantified During Study of Indoor *Vs* Outdoor Activity Budgets in *Propithecus verrauxi*

Activity	Definition	Predict:Inside>Outside
resting	inactive, motionless	DECREASE
scanning*	visual explore/no locomotion	INCREASE
comfort move*	shift position,stretch,scratch	NO PREDICTION
hanging*	suspend motionless	NO PREDICTION
inactivity	pooling of all above	DECREASE
locomotion	vertical cling & leap bipedal hop or walk quadrupedal walk, climb, brachiate	INCREASE FOR ALL
feeding	ingest food or water	INCREASE
autogrooming	use tooth-comb, tongue, or grooming claw on own pelage	NO PREDICTION
allogrooming	groom groupmate as above	NO PREDICTION
playing	swing from rope, rapid ricocheting locomotion, alone or in chase, wrestle	INCREASE
aggression	lunge, cuff, bite toward other	NO PREDICTION
marking	throat-mark (male), anogenital mark "endorsing" (male marks over female's)	NO PREDICTION

* not subjected individually to statistical testing.

The Impact of Naturalistic Conditions

The value of fresh foliage and outdoor housing to captive sifakas is evident at several levels. First, the psychological wellbeing of these endangered primates clearly has been improved by the changes in husbandry described above. Evidence includes the significant reduction of lethargy, accompanied by significant increases in feeding, body weight, and diverse activity, notably including social play. Other studies have implicated play as an important behavioral index of physical and psychological wellbeing (Mason 1965; Harlow 1974; Baldwin & Baldwin 1976; Oliver & Lee 1978). In particular, rejection of play solicitations and failure to initiate play are early signs of distress or illness (observations by MEP on weanling savanna baboons, *Papio c. cynocephalus*, and juvenile ringtailed lemurs, *Lemur catta*; also Fagen 1981). Personal observations during our sifaka program have been as compelling as our limited graphs and statistics.

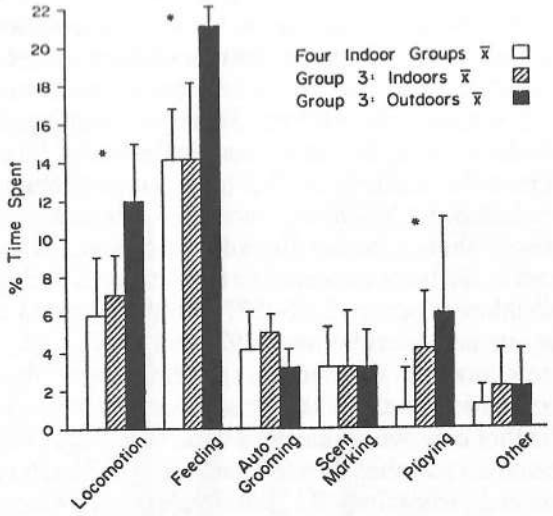

Fig 3: Time spent in 6 activity categories by members of 4 indoor groups and Group 3 (alternately held indoors and outdoors). Group 3 was not one of "4 indoor groups." Bars: group means; brackets: 1 s.d. Asterisks: significant differences.

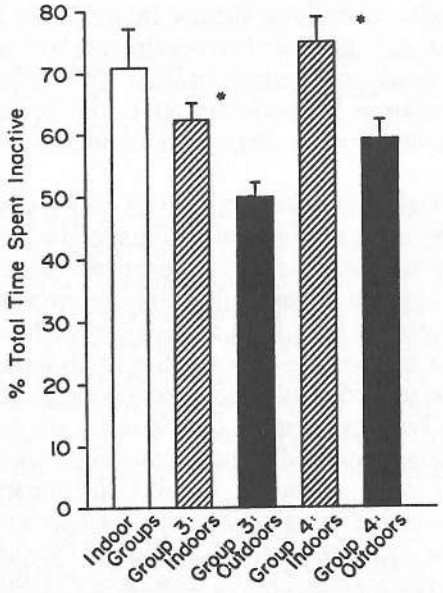

Fig 4: Percentage of time inactive: indoor & outdoor groups. Bars: group means; brackets: 1 s.d. Asterisks: significant differences.

Beyond the added weight and acrobatic play, each sifaka's generally diverse and alert behavior has left no doubt that its psychological wellbeing was improved dramatically by the naturalistic outdoor environment

Second, the long-term impact of the new sifaka management program rests in its ability to maintain good health in these animals while simultaneously boosting the success of their reproductive efforts. Sustained weight gains and a lack of gastrointestinal disorders and other ailments in the sifakas throughout 1986 and 1987 indicate improved health. Remarkably, five conceptions occurred in the sifaka colony between summer, 1985 and summer, 1987. These were the first large steps made toward establishing successful breeding in captive sifakas. Our results stand in sharp contrast to the three conceptions that occurred during the five years preceding the outdoor program (1975-1977 and mid-1982-mid-1985; the colony comprised just one individual between 1977 and 1982).

The ameliorated activity budgets generated by outdoor caging suggested that environments offering still fuller access to natural (istic) sunlight, weather and forage would further improve sifaka welfare and breeding. Therefore, we moved one pair of sifakas into our smallest forest enclosure (0.5 ha) for several months in the late summer and early fall of 1986. The female conceived during that period and gave birth to an infant that survived for four months, the longest period of survival for a sifaka infant conceived in captivity over the previous five breeding periods. Notably, this female and another maintained indoors the previous year produced stillborn infants that year (Table 4). In the spring of 1987, a pair was again placed in our small enclosure and another was introduced to a new 2.25-ha forest enclosure built especially for sifakas. In December 1987 and January 1988, the females of these pairs gave birth to new infants both of which still survive (Table 4). A fourth sifaka born recently at Duke (July, 1986) is now a young adult. Conceived in Madagascar, Sabina joined our colony *in utero*, and she and her mother have occupied one of our large indoor/outdoor complexes since their arrival.

Finally, maintaining our lemurs in forest enclosures allows us to prepare individuals for future efforts to reintroduce these endangered primates to natural ranges in Madagascar. The Duke Center began maintaining *Lemur* social groups in forest enclosures in 1981, when the 0.5-ha enclosure was constructed (Simons 1986; Glander in press). In 1983, 1986, and 1987, we added a 3.5-ha, a 2.25-ha, and a 5.5-ha enclosure, respectively, each containing thousands of trees. Because the Duke Forest is a mix of hardwood and pine species (e.g., *Pinus taeda, P. echinata, Quercus stellata, Cercis canadensis, Liquidambar styraciflua, Liriodendron tulipifera*), our enclosures provide areas comparable in both size and structure to the natural home ranges of lemurs. Conflict due to partial dependence on concentrated provisions is virtually eliminated by delivery of prepared foods to several randomly-selected feeding stations located 75 to 250 meters apart in each enclosure. All the lemurs travel about their "island" habitat with their social groups, supplementing visits to feeding stations with extensive foraging on endemic flora.

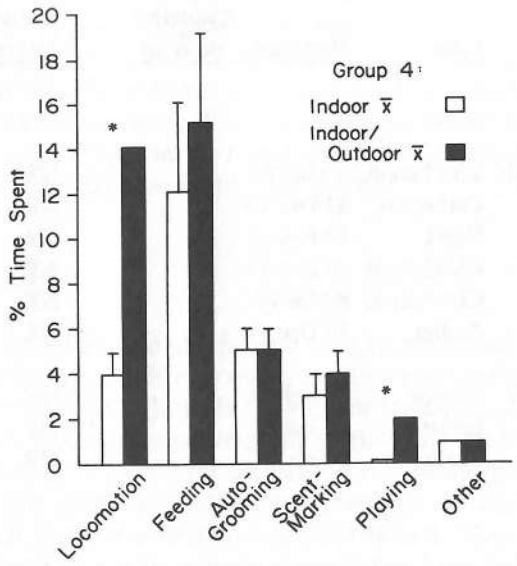

Fig 5: Comparison between indoor & indoor/outdoor study periods for Group 4. Means without brackets: s.d.'s < 1.0. Asterisks: significant differences.

In establishing lemur groups in the Duke Forest, we exchange the great constraints but total security of a cage for the much greater freedom but associated dangers of a semi-wild environment (e.g., raptorial predation, falling from trees). The Duke enclosure projects, however, are an unrivaled success story in captive conservation research with endangered and little-known primates (our four enclosures currently hold eleven groups comprising seven species; Simons 1986). Their naturalistic habitats have promoted mating and effective infant care in every species introduced (Glander in press). After six years, for example, the first group placed in the forest has grown from eight to 31 members. Simultaneously, unsurpassed opportunities have been made available for advanced research into prosimian behavior and reproduction (e.g. Macedonia & Taylor 1985; Taylor & Sussman 1985; Ganzhorn 1986 1987; Macedonia 1986; Pereira & Simons 1986; Taylor 1986; Pereira et al. 1987; Pereira Seeligson & Macedonia in press).

Table 4
History of Sifaka Reproduction at the Duke University Primate Center

Breeding Pair	Infant	Birthdate	Conceived: Captivity or Wild	Housed: Indoors or Out	Lifespan
1970-1977					
Charlotte/Reginald	Charlotte-A	4 May 70	C	NR*	stillborn
	Catherine	31 Dec 70	C	NR	6.3 yrs
	Nigel	10 Feb 72	C	NR	16+ yrs
	Charlotte-B	25 Dec 72	C	NR	stillborn
	Charlotte-C	8 Mar 74	C	NR	stillborn
	Amber	18 Dec 74	C	NR	1.9 yrs
Edith/Sacheverell	Mango	21 Feb 74	C	NR	1.6 yrs
Edith/Nigel	Larke	26 Jan 76	C	NR	0.9 yrs
	Erme	6 Feb 77	C	NR	0.5 yrs
1982-1987					
Theodora/WM	Theodora-A	26 Jun 84	W	I	0.1 yrs
Calpurnia/WM	Calpurnia-A	27 Jul 84	W	I	stillborn
Julia/Augustus	Julia-A	19 Jan 85	C	I	stillborn
	Julia-B	30 Dec 85	C	I	stillborn
Cornelia/Trajan	Cornelia-A	18 Dec 85	C	I	stillborn
	Claudius	5 Dec 86	C	O	0.5 yrs
	Aurelia	8 Dec 87	C	O	LIVING
Flavia/WM	Sabina	7 Jul 86	W	O	LIVING
Octavia/WM	Octavia-A	30 Jun 86	W	O	stillborn
Octavia/Hadrian	Tiberius	20 Jan 88	C	O	LIVING

*: No records are available describing housing regimes for sifakas prior to tenure of ELS as Director of the Primate Center.
W: Conceived in wild C: Conceived in captivity WM: Wild male

Now about 90% of our enclosure animals were born in the Duke Forest. To sample many of their preferred (natural) foods they climb readily to the tops of the highest trees about 30 meters above the forest floor. In fact our forest-living lemurs exhibit skills in foraging and responding to predators as well as in climbing and traveling arboreally that rival those of lemurs in Madagascar. Acquisition of such skills is, of course, essential to success in future efforts to reintroduce lemurs to natural ranges in Madagascar. We are currently developing new agreements with Malagasy officials that will pave the way for reintroduction of captive-born lemurs to protected ranges, perhaps within the next decade.

CONCLUSIONS

Moving social groups of sifakas from generous and well-structured indoor rooms to comparable or even smaller outdoor cages radically changed their behavior. There is little room for doubt that the outdoor housing led to substantial improvements in their psychological as well as physical wellbeing; significant physiological adjustments must have accompanied the observed behavioral changes. Sifakas comprise an important case study of research on captive primates. They (and other rare mammals) have taught us that even relatively good conditions of captivity can impair physiological and behavioral functioning. Housed socially with generous and well-structured indoor space, they become lethargic, fail to reproduce, and sometimes die prematurely. In some way, outdoor living space critically enhances the performance of sifaka neurologic, endocrinologic, and/or gastrointestinal processes. (For effects of housing on brain structure and activity, see Welch 1964; Geller Yuwiler & Zolman 1965; Welch & Welch 1966ab 1968; Bell Miller Ordy & Ralston 1971; also Fox 1986a.)

Biological Dysfunction Under Conditions of Captivity

As yet, systematic efforts have not been made to reveal the biological dysfunctions caused in hardier primates (e.g., macaques) by standard laboratory conditions, conditions characterized by, but not limited to, life-long solitary occupation of caging not much larger than subjects' bodies. For many behavioral biologists, this realization comes as a shock. Scientists aim to reveal facts (or probable facts) by ruling out as many conceivable alternatives as possible through the use of control procedures or observations. Because it is typically impossible for one researcher to corroborate a behavioral study of captive primates with a concurrent or subsequent study of wild representatives of the species, most published research on social behavior is now done either in the wild or under the most

naturalistic captive conditions possible. Nevertheless, results from even remarkably naturalistic captive conditions must be considered preliminary and should be accompanied by the caveat that true field work is needed further to evaluate the significance of results obtained under captive conditions (Pereira et al. 1987; Pereira et al. in press).

Validity of Biomedical Research With Captive Primates

An uncompromising demand from the international research community that appropriate efforts be undertaken to validate the results of biomedical research on primates is long overdue. In primates, or any other animal lineage, physiology and behavior have been co-evolving for millions of years, resulting in myriad bidirectional relationships between these two systems. Because primates are born with an evolutionary legacy of profound and complex gregariousness, it is an inescapable, primary hypothesis for all research on captive primates that documented results substantially reflect idiomorphic responses to housing conditions. It is impossible for scientists working with individually-caged animals to interpret any experimental paradigm before identifying the underlying effects of such housing regimes on the systems that they study. Only by establishing and studying species-typical social groups as control subjects can the extent to which any type of biomedical research is compromised by restrictive, isolate caging be known.

Naturalistic Habitat for Laboratory Primates: General Principles

Alternatively, scientists could take the initiative in improving their research by establishing housing conditions that resemble subjects' natural physical and social environments. A presentation of detailed specifications for particular species is beyond the scope of this chapter; the *type* of change needed is at issue here. We need to begin attending primarily to the needs of subjects rather than only to the needs of researchers. For virtually all primates, physical environments should include branches and branch-like substrata, rather than only shelves and stainless-steel grating. For the most olfactorily-oriented primates (viz. prosimians and some Callitrichidae), substrates must *not* be washed too frequently lest behavioral pathology and skin lesions develop from the over-stimulated "need" to scent-mark. While reasonable rates of air exchange should be achieved, laboratories must not become acoustically uninhabitable. Members of most species exchange low amplitude "contact calls" that communicate individuals' identities and levels of arousal (Macedonia 1986; Pereira 1986); the effectiveness of antiphonal calling can be expected to interact with levels of behavioral disturbance, particularly for immatures. Social environments must include the conspecifics needed for subjects to experience a species-typical social group. Most species naturally exhibit an appreciable range in group composition;

researchers can exploit this natural flexibility for different laboratories and applications. In any group-living situation, however, primates must have opportunities to move periodically into temporary visual seclusion.

The resulting captive environments will have "texture," and regular rearrangement of their physical features is essential to help maintain freshness in that texture. Without such rearrangement (or periodic tranfer of groups among cages), even relatively good cage environments are likely to generate undesirable behavioral stereotypies (e.g., pacing and wheeling; Fox, 1986b) in some individuals. Environmental texture provides colony members opportunities to make choices and exert some degree of control over the quality of their moment-to-moment experience; these are options now known to be essential to psychological wellbeing in primates and other captive mammals (Markowitz 1982; Fox 1986a).

Advantages of Group Housing

Group-housing laboratory primates promises to improve, not jeopardize, the quality of biomedical research in many important ways. Not only will animals' physiological systems be much more likely to perform characteristically, but also researchers will be given opportunities to investigate the natural range of performance of their subject systems, rather than only mean responses of indeterminate validity. Because group-living subjects have opportunities to interact (and to choose not to), their researchers are able to gather otherwise inaccessible behavioral data to identify context-dependent changes and other features of natural variability in physiology. Normative variance must be known before deep understanding of any biological system can be achieved. Moreover, juxtaposition of genealogical records with long-term physiological and behavioral data enhances our understanding of the evolution of physiology, behavior, and the interaction of component systems (Sackett Gunderson & Baldwin 1982).

Housing primate subjects in social groups is not only likely to be necessary for good biomedical research; it is also practical. Outdoor housing for social groups produces demonstrably healthier, less expensive, and much less idiosyncratic subjects (Banerjee & Woodward 1970; Hoffman & Stowell 1973; Bernstein & Gordon 1977). Also, there are methods of housing primates economically in modest indoor social groups that would entail feasible transformation of almost any of the laboratory rooms whose walls are currently lined with rows of isolation cages (Hansen 1976 gives methods used formerly at Rutgers' Institute of Animal Behavior). The many scientists who have worked with group-housed primates at research centers in the U.S. and abroad have the expertise needed to advise laboratory personnel on housing animals more naturalistically while maintaining access to individual subjects (see O'Neill this volume). While some procedural changes will be dramatic, such changes are not always

synonymous with loss of time or increased work. In fact, many methods long used in progressive primate laboratories reduce standard difficulties with physiological research -- difficulties that threaten animal health, technician safety, and data validity. Primate subjects, for example, can typically be trained to present appropriate body parts for vaginal swabbing, rectal exams, and even blood draws.

Whereas our primary objective in writing this chapter has been to illustrate how unlikely it is that either behavioral or physiological systems function normally in primates maintained in isolated, restrictive cages, we hope that we have also been able to provide a new perspective for those who have begun to question whether wild animals, endangered or otherwise, should ever be kept in captivity (Fox 1986b). We believe that work such as that done at the Duke University Primate Center is humane, both daily and over the long term, for the individual primates involved. Moreover, such efforts are likely to prove invaluable for the future of their species.

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Family: Lorisidae (Lorises)
Tarsiidae (Tarsiers)
Cebidae (New World Monkeys)—*Aotus*

— 5 —
Psychological Well-Being of Nocturnal Primates in Captivity

Patricia Chapple Wright, David Marsland Haring, Mary Kathryn Izard, and Elwyn LaVerne Simons

INTRODUCTION

Nocturnal primates including *Aotus* and *Galago* are being increasingly used as laboratory animals. There are approximately 3,000 owl monkeys and 500 *Galagos* in the US that are used primarily in biomedical research. Because of their large eyes relative to body size these night-active animals are often preferred for studies of vision. The importation of wildcaught animals for research has become increasingly difficult and inadvisable from a conservation point of view, and it is preferable to obtain captive-bred animals from breeding colonies for research needs. Any understanding of the social behavior and psychological needs of these night-active primates will produce better breeding results and healthier, better-adjusted subjects. There are over 30 species of nocturnal primates, many of which have never been kept in captivity. For this chapter we have selected three genera as case studies. Two (*Aotus* and *Galago*) are frequently used in biomedical research, and the third (*Tarsius*) has only recently been shown in zoo exhibits. We hope to explain how a knowledge of the behavior, diet and habitat preferences of these primates in the wild can give us useful insights into keeping these nocturnal primates healthy and breeding in captivity.