FINAL REPORT ON ENVIRONMENT ENHANCEMENT TO PROMOTE THE PSYCHOLOGICAL WELL-BEING OF NONHUMAN PRIMATES

U. S. Department of Agriculture
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This Final Report contains the scientific basis for the Draft Policy and the methods we used in developing the Draft Policy. To view the Draft Policy and request for comments that was published in the Federal Register on July 15, 1999, click on Pdf

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I. INTRODUCTION AND PROJECT HISTORY

This report provides Animal and Plant Health Inspection Service (APHIS) Animal Care employees, the facilities they regulate, and the public with a policy on environment enhancement to promote the psychological well-being of nonhuman primates. The policy is an interpretation of the regulation published in 9 CFR, Part 3, Subpart D, §3.81. This report explains the scientific basis for the policy and how it was developed. It consists of the following:

- **Chapter I. Introduction and Project History**

Reviews background of the project to develop the policy: how it was initiated, the methods used, and the results of surveys and interviews.

- **Chapter II. Promoting Psychological Well-Being**

Explains the Animal Welfare Act, the language of U.S. regulatory standards, other nations' requirements regarding primates' psychological needs, the difficulties inherent in measuring psychological well-being, and the reason why this policy relies on species-typical noninjurious behavior as the primary indicator of psychological well-being.

- **Chapter III. Critical Element Concept**

Introduces the concept of categories of primate behavioral needs and explains that there are environment enhancement strategies or elements that correspond to each. Gives the critical elements to be addressed in each environment enhancement plan for captive primates.

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- **Appendix A. 9 CFR Section 3.81 Environment Enhancement to Promote the Psychological Well-Being of Nonhuman Primates**

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- **Appendix C. Glossary**

Defines special terms frequently used in this report.

A. Background on Evaluation of the Performance-Based Standard for Nonhuman Primates

Performance-based standards in Animal Care have been controversial since their inclusion in the 1985 Amendments to the Animal Welfare Act.[(1)] In 1991, when USDA, APHIS adopted Title 9 of the Code of Federal Regulations (CFR), Part 3, Subpart D, "Specifications for the Humane Handling, Care, Treatment, and Transportation of Nonhuman Primates", it included Section §3.81 called, "Environment enhancement to promote psychological well-being of nonhuman primates." (See Appendix A for the text.) After about five years, APHIS conducted an internal

evaluation[(2)] of the performance-based standards. It administered a brief mail survey of its Animal Care field employees about their opinions and experiences applying these standards. The survey results indicated a number of concerns regarding the effectiveness of the standards for environment enhancement of nonhuman primates.

Many of the opinions expressed by Animal Care employees in the 1996 survey centered around a lack of clarity and specificity in the standards and a perceived lack of enforceability. Almost half the responding employees felt that the criteria in the regulations were not adequate for facilities to understand how to meet them and for inspectors to judge if a facility was in compliance. About two thirds of the responding employees suggested additional criteria or items that should be in a facility's primate enhancement plan. Twelve employees proposed some specific requirements on social grouping, primary enclosure space, foraging opportunities, novelty, or other environmental features.

The 1996 study report offered some recommendations on how to improve the effectiveness of the standards, including:

- Guidelines should be developed by Animal Care to clarify and provide more structure to the existing standards; and
- Documentation should be required of facilities to demonstrate continued effectiveness of their primate enhancement plans.

As a result of these recommendations, APHIS's Animal Care Management Team assigned a team of Animal Care field employees to develop a model for primate environment enhancement and a policy for inspectors and facilities. Their goal was to retain the performance-based approach, and maintain a balance between the Agency's need for inspection practicality and enforceability and its need for flexibility and results-orientation. It is hoped that the interpretive policy developed as a result of this team's work will assist in the fair application and enforcement of the environment enhancement standard.

B. Team Methods

APHIS Animal Care's Primate Environment Enhancement Team was formed in March, 1997. It was composed of five Veterinary Medical Officers, an Animal Care Inspector, a Regional Director, a resource specialist from USDA's National Agricultural Library's Animal Welfare Information Center, the coordinator of APHIS Animal Care's Strategic Direction initiative, and an anthropologist from APHIS's Policy and Program Development. They are, alphabetically, Tim Allen, Ruth Bakker, Lisa Bellamy, Charlie Currer, Greg Gaj, Betty Goldentyer, Betsy Lyons, Natalie Roberts, Sylvia Taylor, and Dick Watkins.

From March, 1997 to March 1998, the Enhancement Team embarked on an extensive review of the professional primatology literature, a number of facility primate enhancement plans, and some enforcement case histories. Comments made by employees in the 1996 mail survey were reviewed. A number of respected professionals, knowledgeable about primates, were consulted.

During the early phase of the project, members of the Primate Environment Enhancement Team needed to understand their colleagues' opinions more clearly and in more detail than could be derived from the 1996 employee survey data. To supplement the information collected, the team members contacted 21 other Animal Care field employees who inspect primate facilities. They interviewed them regarding current conditions at the facilities they inspect that house primates. They asked what the problems are and what should be required of facilities to improve the care of primates. These in-depth interviews revealed that certain inadequate environment enhancement conditions and practices persist at regulated facilities although the 1985 amendments to the Animal Welfare Act were intended to minimize these conditions or practices. The inspectors echoed many sentiments expressed in the 1996 mail survey and called for guidance that would provide more structure and specificity and clarify the minimum quantity and quality of enrichment that will be enforceable.

In a series of conference calls and meetings, the Primate Environment Enhancement Team developed a conceptual model and a policy. Members also drafted this discussion and the supplementary materials shown in the appendices that are intended to aid inspectors and regulated parties. The Enhancement Team members circulated the draft materials for comment and revision to colleagues at the Animal Care Employees National Work Conference in Riverdale, Maryland in March, 1998, and to the Supervisory Animal Care Specialists and Animal Care Staff in August, 1998. The team tested the application of the proposed policy by visiting four facilities, and as a result, made several modifications to the policy.

In preparation for the document's release to the public for comment, it was reviewed by several members of USDA management and federal partners. Modifications were made to ensure the policy's enforceability and consistency with other policies and the report's readability and proper form. A decision was made to call the new document a "policy" rather than "guidelines", as it had been referred to up to this point. The accompanying *Federal Register* documents were developed.

The Team would like to acknowledge and thank many people who have contributed to the development of this document so far. Researchers, librarians, and consultants have provided copies of publications. Facilities, associations, and animal interest groups have provided background information and expressed their opinions. APHIS Animal Care inspectors and Supervisory Animal Care Specialists have reviewed earlier drafts and provided feedback. They facilitated the field visits. Other staff members in Headquarters have facilitated the clearance of the policy, assisted with production, distribution, and communications. USDA's National Agricultural Library has provided editorial advice. In particular we would like to thank: Janet Baer, Kate Baker, Mollie Bloomsmith, Sue Boinski, Linda Brent, Cobie Brinkman, Allegra Bukojemsky, John Cant, Douglas Cohn, Debra Forthman, Nelson L. Garnett, Marisa Garza Schmidt, Larry Jacobsen, Michael D. Kreger, Jean A. Larson, Barbara Lester, Trevor

Poole, Viktor Reinhardt, David Seelig, and Lucy Lerner Wormser. While these individuals were very helpful in providing their input, they are in no way responsible for the text of this document or the policy, in whole or in part.

C. Results of Surveys and Interviews

Below is a summary of issues raised in both the mail survey and telephone interviews of APHIS Animal Care employees.

1. Minimum Criteria Need Clarification

The standards in 9 CFR §3.81 emphasize the presence of a physical document called an "environment enhancement plan for primates" at each facility, but the standards contain few solid criteria on which an inspector can judge the content of the plan as "in compliance" or "out of compliance". The regulations state that the plan must address social grouping, enrichment of the physical environment, special considerations, and restraint devices, but what is required in order to address these in a minimally compliant manner is unclear. Some inspectors said they had the impression that the only legally necessary condition for compliance was the existence of the document itself, regardless of its contents. A few commented that once the facility's attending veterinarian approved a plan, it was problematic to enforce additional requirements, even if that plan was very poor.

A few inspectors expressed the concern that without adequately specified criteria and only a notion of an abstract endpoint to achieve (psychological well-being, which can not be directly or unequivocally measured), facilities are free to try, or NOT try, anything--including a very behaviorally restrictive, barren environment. No one, including inspectors, would have any basis for criticism, until there is proof of "poor performance". Unfortunately, there is no agreement on what "poor performance" looks like. There might be virtually no performance parameter or outcome that could be proven to have been caused by an inadequate environment.

2. Lack of Enforceability

APHIS Animal Care employees recognize that there is a legal question concerning the enforceability of performance standards. Some inspectors said they could recognize a plan that was not in accordance with professional literature or was not "adequate to promote psychological well-being". However, they had concerns about Agency support for particular interpretations or judgment because of the vague language and nature of the performance standard.

3. Minimalistic and One-Sided Enhancement Programs

A common refrain among inspectors was that too many enhancement programs consisted of only one or two types of enrichment, such as feeding of treats or provision with a simple rubber toy, in an otherwise barren, stimulus-poor environment. There is agreement that acceptable enhancement programs should stimulate a variety of normal activities and meet all major areas of behavioral need in a species-typical manner, rather than concentrate on a few limited aspects of behavior (Olfert *et. al.* 1993, Poole 1991b). Many employees supported the idea that enhancement programs be required to address several different aspects of a primate's environment and behavior, beyond the superficial breakdown given in 9 CFR §3.81 ("social", "physical", and "special"). The team received many helpful suggestions on this issue.

4. Questionable Implementation of the Facility Plans

Another problem has been the difficulty in proving actual implementation of an enhancement plan. Animal Care inspectors recommended facilities be required to provide better documentation of implementation.

5. Low Levels of Appropriate Social Grouping

Some Animal Care inspectors felt that there were too many singly housed primates. This is especially true at research facilities and among small licensed exhibitors. Inspectors who inspected public exhibits with singly housed chimpanzees said that the reasons most frequently given for housing these animals singly were that the exhibitor: preferred to have only one chimpanzee at a time; considered them more tractable when single-caged; was ill-equipped to permit socialization of one single-caged chimpanzee with another; and/or was unwilling to transfer or loan a single chimp to other facility, even one equipped to provide a socially enriched environment. All of these reasons reflect convenience for the owner(s), not primary consideration for the psychological needs of the animals.

6. Practices that Perpetuate Socially Incompetent Individuals or Abnormal Behavior

Animal Care inspectors were concerned that dealers involved in the pet trade continue to remove infants from their care-giving parent(s) at an inappropriately early age, for reasons other than medical necessity. These practices are known to produce socially incompetent adults and contribute to the low levels of social grouping already identified.

7. Poorly Furnished Environments

Inspectors reported facilities with cages that did not have a single elevated perch, shelf, or similar structure. Inspectors said they often did not cite the above situations as noncompliant in inspection reports, although they believed the situations were not in accordance with the intent of the Animal Welfare Act, because they believed the Agency could not or would not support them.

Inspectors mentioned other problems with enhancement plans. Some plans are static, not updated to reflect whether they are working effectively. Some are not updated to be consistent with changes in the facility's population and use of animals. Some plans do not consider variation in individual animals' personalities and rearing histories. Others fail to avoid latent effects of harmful housing or rearing conditions. Inspectors said some facilities solve the problem of abnormal or psychological distress-related behavior by simply selling or transferring the primates to other parties. Facilities that sell or transfer primates after relatively short periods of use have little motivation to concern themselves with cumulative or latent effects on the behavior of their primates because these behaviors will be manifested at another facility.

The urgency of these problems or issues raised by their colleagues motivated the members of the Primate Environment Enhancement Team to move forward with the design of a conceptual model and policy. Another factor they had to consider was how to promote psychological well-being for nonhuman primates in the context of the larger political environment. A strategy had to be developed to fulfill the original intent and language of the Animal Welfare Act, while considering the response of the community affected by any new policy, the approach of other nations and societies also facing similar problems, and the difficulties inherent in scientifically measuring psychological well-being. These topics are discussed in Chapter II.

II. PROMOTING PSYCHOLOGICAL WELL-BEING

A. Intent and Language of the Animal Welfare Act

The Animal Welfare Act states that "The Secretary [of Agriculture] shall promulgate standards... The standards.. shall include minimum requirements .. for a physical environment adequate to promote the psychological well-being of primates" [AWA Sec. 13 (a)(1), emphasis added.]

The Animal Welfare Act was intended to promote the psychological well-being of nonhuman primates, not just prevent abnormal behaviors from occurring. Because there were no standards for primate psychological well-being prior to 1991, no measurable comparisons can be made as to whether the use of performance-based standards has improved the welfare of the animals as intended. As previously stated, most inspectors feel the lives of primates have been improved some, but that overall not enough is being done to provide a "physical environment adequate to promote the psychological well-being of primates", especially in the area of social grouping.

The concept of psychological well-being does not lend itself to precise definition. Facilities are allowed latitude in how they meet the requirements, as long as they achieve the desired results or outcomes. Therein lies the problem, as no one has defined the results desired in terms of something that can be easily observed and recognized.

Some facilities claim their environment enhancement programs are adequate because there are no distressing behaviors or appearances of ill health with their primates. This is a short-sighted view since waiting to improve a minimally enriched environment until a primate starts showing signs of psychological distress was not the intent of the Animal Welfare Act.

The Primate Environment Enhancement Team believes the intent of the Animal Welfare Act was to provide nonhuman primates with the opportunity to express a wide range of non-injurious, species-appropriate behaviors. The team's goal with this policy is to re-emphasize attention to adequate environmental conditions before abnormal behaviors develop.

B. Community Response

Both the regulated community and the interested public have responded to the increasing awareness of the importance of the psychological well-being of nonhuman primates. There is now a wealth of scientific and anecdotal information on the topic. The exhibition and research communities have sponsored scientific research and professional meetings to further knowledge of the subject. The National Research Council (NRC) Institute for Laboratory Animal Research (ILAR) recommended ways in which to assess and promote psychological well-being. The NRC independently arrived at many of the same points that APHIS has arrived at and its 1998 report is an excellent resource for most purposes. "The purpose of this volume is to help scientists, veterinarians, curators, inspectors, duly appointed committees, and others concerned with the psychological well-being of nonhuman primates to deal more effectively with this complex issue" (NRC/ILAR 1998:4).

At the same time, there has been concern over the implementation of the provisions, and members of the public and an animal welfare organization brought a legal suit against USDA [Animal Legal Defense Fund, Inc. *et. al.* v. Daniel R. Glickman (Docket Nos. 97-5009, 97-5031, and 97-5074).]

C. Other Nations and Societies

There is a movement in other nations and professional societies abroad to develop similar provisions for meeting primates' psychological needs. Some have specific recommendations or requirements for achieving them. Jones (1996) has reviewed and compared recommendations of three

major bodies influencing European laws on primates produced, held or used for research: the IPS (International Primatological Society 1993); the PVEN (Primate Vaccine Evaluation Network) (Poole and Thomas 1995); and the Berlin Workshop, an international workshop on the Accommodation of Laboratory Animals in Accordance with Animal Welfare Requirements held in Berlin, Germany in 1993 (Poole *et. al.* 1994). Common to all are the following:

1. Physical, physiological, and behavioral needs must be satisfied.
2. The environment must contain sufficient useable space, complexity, and enrichment.
3. Social housing should be the general rule and individual housing should be the exception.
4. The environment should promote a species-appropriate repertoire of behavior.
5. Primates should not be weaned from their mothers at an age that will produce psychological abnormality, prior to 6 months of age.

In addition, the PVEN emphasizes providing climbing structures and vertical space, novelty in the animal's environment, and giving the animal opportunity to exercise control over some aspects of its environment. The Berlin Workshop (Poole *et. al.* 1994) specifies provision of sleeping boxes, climbing structures, and gnawing wood for Callitrichidae (marmosets and tamarins); environmental novelty and variety; and the use of animal training to decrease the stress of handling. It also gives minimum space requirements. Although these requirements are divided into slightly different weight classes than USDA's requirements are, the minimum dimensions required by the Berlin Workshop are generally 1.5 to 3 times larger than USDA's minimums. The Berlin Workshop also states primates kept for long periods should be housed in even larger spaces, but it does not define what constitutes a "long" period.

The United Kingdom Code of Practice (Home Office 1989) contains language that is more specific. The cage volume should enable the animal to exhibit vertical flight reactions, jump, climb, and sit on perches with neither its head nor its tail touching the cage. For Callitrichidae, it specifies "wooden perches, a swing, a wooden nest box, a shelf for feeding, and sufficient shavings to allow foraging." The animals should also be allowed to "jump horizontally from one perch to another." The same cage structures are specified for arboreal, polygamous primates, such as squirrel monkeys. Group-housed macaques and baboons must be given escape routes, sleeping areas with several entrances, and multiple food and water stations.

The Canadian Council on Animal Care (CCAC) provides minimum cage space requirements for primates in research that, for most species, are the same or slightly larger than U.S. minimums. Single housing is "strenuously discouraged" (Olfert *et. al.* 1993). A number of other recommendations are made with respect to social grouping, cage enrichment, exercise and foraging activities (Olfert *et. al.* 1993).

The Australian National Health and Medical Research Council's (NHMRC) official policy requires the following: appropriate social grouping, unless individual caging is justified by an animal ethics committee; grooming opportunities for individually housed primates; access to outdoor enclosures for animals held longer than six weeks; training of isolated animals to facilitate handling; adequate enclosure size to accommodate group housing and varied activities; and foraging opportunities (National Health and Medical Research Council Animal Welfare Committee 1997).

The laws and regulations of some nations concern themselves with the specifics of primate environment enhancement just as the U.S. policy being developed here does. However, they differ from it in other ways. One of these is the animals to which the requirements apply. In the U.S., the enhancement regulation applies to all primates in facilities regulated by USDA. The requirements apply to primates in zoos and circuses as well as to primates in research[(3)], breeding, and many other types of facilities. In Europe, the housing of primates in zoos is governed by standards developed under the UK Zoo Licensing Act of 1981 and/or the 1994 standards of the European Association of Zoos and Aquaria (EAZA). These regulatory documents for zoos are far more general than the other European regulatory documents reviewed above, which apply to animals in research laboratories. The EAZA standards state that the welfare of zoo animals is a matter of both "physical and social well-being" (EAZA 1994). Both the UK Zoo Licensing Act standards and the EAZA standards require the provision of enclosure space and environmental structures and substrates appropriate to the needs of the species.

Developing regulatory language with specific details about environment enhancement does not appear to have caused serious problems for the nations above who have tried it (Boisvert 1997, Poole 1997a, and Popovic 1997). In the present era of increasing concordance in regulatory matters to facilitate international trade and commerce, it will be advantageous for the U.S. to adopt criteria and language that will meet with acceptance by other nations.

D. Difficulties Inherent in Measuring Psychological Well-being

The ultimate objective of 9 CFR §3.81 is "psychological well-being" (PWB), a subjective state experienced internally by each animal. It is difficult to define this term and currently there are no ways to measure it directly. Working definitions presume characteristics that are manifested in various indicators (Broom and Johnson 1993, Duncan *et. al.* 1993, Mason and Mendl 1993, Novak and Petto 1991b, Poole 1992).

The indicators that have been proposed include: (1) physical values such as longevity, growth rate, reproductive success, hair coat, and body condition, etc; (2) physiologic values such as heart rate, blood pressure, body temperature, levels of serum cortisol and other hormones, and rates of lymphocyte proliferation or suppression; (3) behavior; or (4) a synthesis of many such measures, perhaps weighted by evolutionary or other contexts (Boinski *et. al.* 1999, Broom and Johnson 1993, Line 1987, Snowdon and Savage 1989).

The assessment of the PWB of each primate relies to some degree on subjective interpretation of these indices, some of which may suggest opposite conclusions (Mason and Mendl 1993, Sackett 1991). For example, Coe found that a change in the social environment of older rhesus monkeys produced positive behavioral changes, but also evidence of reduced immune competence (C. L. Coe 1991). An ideal approach would combine many different measures and take into account differences between individual animals. This is often not feasible and the measurement of many of the parameters would be unnecessarily invasive.

An animal's behavior is still the index most commonly accepted for assessing PWB. It is also the index most readily and consistently available (Olfert *et. al.* 1993, Poole 1991b). To assess PWB, one may look at the animal's general activity level, the percentage of time it spends doing various things, its use of cognitive skills, its maternal behavior, locomotor behavior, play, communication, appetitive and self-maintenance behaviors, its avoidance of predators, its response to novelty and routine husbandry, affiliative behavior, and vocalizations. Environmental effects on vocalizations may provide a rich opportunity for psychological assessment that is only beginning to be applied to animal welfare (Crowell Comuzzie 1993, Mulligan *et. al.* 1994).

How can the welfare implications of an animal's behavior be interpreted and what does it tell about the adequacy of its environment? The performance of abnormal behaviors, such as stereotypies, is interpreted to reflect a lower level of well-being and an inadequate environment (Bayne *et. al.* 1992a, Broom and Johnson 1993, Maple 1979, Olfert *et. al.* 1993). Some may assert that the absence of such behavior indicates well-being and therefore an adequate environment. But stereotypies do not always indicate current suffering or currently inadequate environments. Current abnormal behavior may reflect past, not present, environments (Brent and Hughes 1997, Broom and Johnson 1993, G. J. Mason 1991a and 1991b, Mason and Mendl 1993). Two conditions known to result in aberrant behavior that may persist into adulthood or be expressed long after infancy are: (1) restricted social environments during development; and (2) early infant separation from the mother. Some aberrant behaviors resulting from these conditions are resistant to treatment (Capitanio 1986, Mason and Berkson 1975, Novak and Drewson 1989:166, O'Neill 1989). Some are eventually reversible after considerable ameliorative efforts (Fritz 1989, Kessel and Brent 1997).

This underscores the importance of directing major regulatory efforts toward requiring environments and practices less likely to be associated with the expression of aberrant behaviors, either immediately or later in life. Put in a constructive way, facilities should be required to enhance the environment of nonhuman primates in a way that promotes the expression of a wide variety of positive, normal behaviors. Prevention is better than treatment, in mental health as in physical health (Schapiro *et. al.* 1996a). The USDA's obligations under the Animal Welfare Act include requiring standards aimed at prevention of problems.

The performance of stereotypies remains an important and valid indicator of welfare problems for most situations (Broom and Johnson 1993, Olfert *et. al.* 1993, Toates 1995, Wemelsfelder 1993). The benefit of any interpretive doubt should go to the animals (Bekoff 1994, Duncan *et. al.* 1993). Many authors have concluded that welfare should also be seen as more than just absence of negative behavior (Bayne 1989:27, Broom and Johnson 1993, Poole 1992, Segal 1989 Preface). The expression of species-typical or species-appropriate behavior should be the goal of an enhancement program.

There has been some debate about whether normal behavior reflects adequate well-being or whether the performance of specific behaviors themselves is necessary to cause well-being (Petherick and Rushen 1997, Veasey *et. al.* 1996). In either case, it is important that USDA regulations require facilities to provide captive primates with an environment where they can express a wide range of normal behaviors.

E. Species-Typical Behavior (STB)

USDA regulations state, "The physical environment in the primary enclosures must be enriched by providing means of expressing non-injurious species-typical activities" [U. S. Department of Agriculture, Animal and Plant Health Inspection Service 1998: 9 CFR 3.81(b)].

What constitutes STB or a normal behavioral repertoire in captivity? A primate in captivity will not be able to exhibit the full range of behaviors that occur in nature. Colony managers would not want to promote infanticide or harmful aggression. The primate itself would not wish to suffer infanticide, predation, or other conditions that sometimes occur in nature. In passing the Animal Welfare Act, Congress did not intend such extremes to be promoted in the maintenance of captive primates. Therefore, in this policy, the term "species-appropriate behavior" has been adopted instead of the more common term, "species-typical behavior."

The pitfalls of attempting to stimulate every natural behavior have been discussed by Veasey *et. al.* (1996). (See also Rosenblum and Andrews 1995.) Putting aside the extremes, behavior observed in nature serves as one of the most useful guides to what a captive environment should allow (McGrew 1981). Observations of captive but free-ranging primates may provide the best of both worlds (Newberry 1995, O'Neill *et. al.* 1990). Environmental preference testing can also be used to clarify the picture (Bayne *et. al.* 1992a, Line 1987). As Kaumanns (1997) stated, captive conditions "should still fit within [the] adaptive potential" of the animal. Differences between individuals of a species, as well as between species, must also be taken into account (Clarke and Boinski 1995, Laudenslager and Boccia 1996, Suomi and Novak 1991).

In summary, although difficulties are inherent in applying USDA's regulation concerning environment enhancement to promote the psychological well-being of nonhuman primates, we have learned a great deal since the amendments to the Animal Welfare Act were passed in 1985 and 9 CFR §3.81 was adopted in 1991. USDA now has a basis for creating more specific guidance on environment enhancement and for bringing the U.S.

program into step with international developments. The central idea is that nonhuman primates must be given an environment in which they can express the wide range of behaviors practiced by others of their species in nature. Their captive environments must be enhanced to give them opportunities to exhibit these behaviors. When such conditions are achieved, the intent of the Animal Welfare Act to promote their psychological well-being will be fulfilled.

III. CRITICAL ELEMENT CONCEPT

There is a consensus emerging in the literature on primate enrichment that "species-typical" or "species-appropriate" behavior should be the goal of enhancement programs, and that it is important for the animal to be able to express a "normal repertoire" or a "full range" of normal behavior--a range that is complete and balanced (Brent and Long 1995, Brent and Stone 1996, Chamove and Anderson 1989, Fragaszy 1991, Olfert *et. al.* 1993, Poole 1991b and 1992, Rose 1994, Toates 1995, Line 1987). Scientists believe that it is not enough for individual or groups of primates to express just a few "normal" behaviors. Environments should be complex enough to allow a variety of activity and stimulus-response options. Also, it is difficult to interpret an animal's behavior and activity levels if it has relatively few realistic choices of behavior in that environment.

Captive animals are limited in their ability and/or motivation to move about freely and carry out many of the behaviors their species normally exhibit in a natural environment. As stated in Chapter 1, USDA inspectors have found that many current enhancement programs are narrow and address only one or two aspects of the animal's life. In order to correct this problem, USDA must stimulate the addition of diverse environmental elements that can promote a wider repertoire of species-appropriate behavior. This need has motivated the Primate Environment Enhancement Team to develop the concept of critical elements.

There are distinct categories of activity or behavior, each of which should be present to some extent to round out a normal behavioral repertoire. Similarly there are categories of enhancement strategies or elements of an environment that address these behavioral needs and/or promote the expression of these behaviors. Such categorizations are useful for providing structure to an enhancement program and to regulations and policies. Numerous sources in the primate enrichment literature show similar categorizations of these elements (Bloomsmith *et. al.* 1991, Bowden 1988, Keeling *et. al.* 1991, Line 1987, Maple 1979a, Newberry 1995, Olfert *et. al.* 1993, Poole 1992 and 1998, Rosenblum and Andrews 1995, Schapiro and Bloomsmith 1995). They share the idea that it is critical to touch upon each element appropriately, rather than concentrate on one or two aspects of the normal behavioral repertoire.

The National Research Council in its report on *The Psychological Well-Being of Nonhuman Primates* discusses four main determinants of psychological well-being:

Beyond reasonable physical well-being, psychological well-being is enhanced by

- Appropriate social companionship.
- Opportunities to engage in behavior related to foraging, exploration, and other activities appropriate to the species, age, sex, and condition of the animal.
- Housing that provides for suitable postural and locomotor expression.
- Interactions with personnel that are generally positive and not a source of unnecessary stress. (NRC/ILAR Report 1998:2)

The report emphasizes the importance of flexibility since no single approach will be effective for all animals. Measuring and validating the effectiveness of an environment enhancement program is also vital to ensure that psychological well-being is actually improved.

Nevertheless, a comprehensive program to improve the psychological well-being of nonhuman primates **will attend to each of the variables and include a means to test and assess the influence of each** [NRC/ILAR Report 1998:2, emphasis added].

Other documents outline similar methods with several elements or variables (International Primatological Society 1993, Olfert *et. al.* 1993, Poole *et. al.* 1994, Poole and Thomas 1995).

These differ vastly from minimalist programs in which facilities adopt a single element such as feeding food treats as the mainstay of their enhancement, while keeping the enclosures barren and neglecting other environmental features. Minimalistic programs such as these do not stimulate a wide range of species appropriate behaviors and probably increase the potential for obesity. A recent study by Boinski *et. al.* (1999) exemplifies the importance of variety and a minimum level of enrichment. Providing both a foraging device and two toys to single housed *Cebus apella* markedly increased species-appropriate behavior and decreased abnormal behavior. These behavioral changes were correlated with expected effects on plasma cortisol. The overall positive effect was dramatically greater with both of these enrichments than it was with either enrichment alone, and the baseline environment already included cage furniture and daily multiple feedings of standard diet and treats.

One-sided programs have persisted at some regulated facilities because the current USDA regulations appear to allow them. Stimulation of only one type of normal behavior should not be considered adequate for compliance. Such programs can be compared to a diet that contains an excess of

some nutrients and inadequate levels of others. A nutritionally balanced diet will provide certain vitamins and minerals plus a number of calories distributed among different forms of metabolizable energy. A food pyramid can be constructed to represent the relative importance of the essential food groups. A variety of individual foods are available within each food group to provide the necessary nutrients in appropriate proportions. Many food items are equivalent in value, but some are more palatable or costly than others.

This food pyramid model is analogous to the critical element concept in the Primate Environment Enhancement policy being developed for USDA here. The policy states that five elements are critical to environments that adequately promote the psychological well-being of nonhuman primates:

1. Social grouping
2. Social needs of infants
3. Structure and substrate
4. Foraging opportunities, and
5. Manipulanda.

A minimally acceptable program of environment enhancement will contain all five. A given enhancement strategy or environmental feature may simultaneously address more than one element. The extent to which each enhancement strategy may be deemed to satisfy more than one element simultaneously is a matter of professional judgment and should be evaluated on a case-by-case basis. In addition to the five critical elements, any enhancement plan should give consideration to two other aspects of the environment: stimulating all five senses; and providing the animal novelty and control over aspects of the environment.

Regulated facilities must target each critical element in their primates' environments, address it in their plan, and implement the plan in a balanced way. To meet the desired objective for each critical element, a variety of options exist. The options chosen should be appropriate for the species and individual characteristics of the animal as well as its intended use by the facility. The facility must observe the effects on the animals' health and behavior and continue to make modifications as necessary.

The essence of the performance-based standard approach is that regulated facilities assume responsibility for the end results and are given flexibility in how they approach achieving them. For this to be successful, facilities must clearly understand the goals and try different methods until they get the desired results.

We believe the majority of regulated facilities intend to voluntarily comply with the law to the extent they are able. However, educational efforts alone are not sufficient to gain compliance. There always exist some facilities that must be compelled by enforcement. USDA cannot overlook the failures of members of the second group or it will hurt the members of the first group. Fairness in government requires that if regulations exist, they are enforced uniformly and consistently. Those who voluntarily comply with the intent of the law should not be penalized for it by suffering a disadvantage relative to others who circumvent regulations.

In order for minimum standards to be enforceable, the standards must have definition and structure. It must be clear to all facilities when violations occur and enforcement action is necessary. The concept of minimum criteria has been useful in government regulations because it objectifies what is unacceptable and increases fairness. Some regulatory areas such as primate psychological well-being are so complex that specifying criteria in detail would require volumes of legal language and years to develop. There will always be the need for the careful judgment of a qualified professional who is trained in Agency policy based on regulatory experience, ethics, and applied ethology. USDA's policy has been developed to capture these principles and while allowing facilities as much flexibility as necessary.

IV. LITERATURE REVIEW AND DISCUSSION

In order to develop the new policy on environment enhancement to promote psychological well-being of nonhuman primates, USDA's Primate Environment Enhancement Team conducted a review of professional literature related to the ecology, natural history, and behavior of primates. The findings of this literature review are presented and discussed in the order the five critical elements are listed in Chapter III: social grouping; social needs of infants; structure and substrate; foraging opportunities; and manipulanda. After the five critical elements are discussed, findings are presented for two additional considerations that should be built into each environment enhancement plan--sensory stimulation, and novelty and control. This chapter is intended to explain the reasons for the policy, but it may also be useful to those who own primates and wish to understand their needs generally before beginning a detailed quest for information on the species in their care.

The team reviewed publications of scientists who have observed primate behavior in nature and under zoo and laboratory conditions. It also looked for advice and strategies directed to those who manage colonies of primates. It sought to understand what scientists and practitioners today know about each critical element and what the requirements to each one should be. The field of knowledge has grown tremendously since the Animal Welfare Act's 1985 amendments were passed. The number of articles published is increasing every year, as are the number of electronic mail discussions and sites on the World Wide Web devoted to the topic. Although the team was not able to survey all the literature, it was able to review enough sources to draw conclusions about what environmental conditions promote the psychological well-being of nonhuman primates. Sources are listed at the end of this paper. The interested reader who is unable to locate information sought may try the Animal Welfare Information Center of the National Agricultural Library, 10301 Baltimore Boulevard, Beltsville, Maryland 20705, (301) 504-6212. The Center's Email address is:

AWIC@NAL.USDA.GOV. For document delivery, another resource is the Wisconsin Regional Primate Research Center Library at the University of Wisconsin in Madison, Wisconsin 53715-1299, (608)263-3512. The Email address is: jacobsen@primate.wisc.edu. The webpage address is: http://www.primate.wisc.edu/pin/primpro.html. The Primate Information Center at Box 35730, University of Washington, Seattle, WA 98195-7330, (206) 543-4376, is an indexing service for scientific literature on all aspects of nonhuman primate research. Its manager, Jackie Pritchard, is at: plj@u.washington.edu. The webpage address is: htt://www.rprc.washington.edu/pic1.htm.

A. Social Grouping

1. The Social Nature of Primates

USDA regulations state that, "The environment enhancement plan must include specific provisions to address the social needs of nonhuman primates of species known to exist in social groups in nature." [U. S. Department of Agriculture, Animal and Plant Health Inspection Service 1998:9 CFR §3.81(a)].

Social interactions are considered to be one of the most important factors influencing the psychological well-being of most nonhuman primates. (NRC/ILAR Report 1998:13)

Nearly all primates have some tendency to seek the company of their own kind at times other than mating (McGrew 1981, Rowe 1996, Pereira *et. al.* 1989b, Fleagle 1998). Even within those few species known as "solitary"--orangutans and most nocturnal prosimians--individuals of certain age or sex classes can still be found in social associations at certain times (Bearder 1987, Rodman and Mitani 1987, Rowe 1996, Van Schaik and Van Hoof 1996). Despite their solitariness in the wild, adult orangutans have been kept in compatible social groups in captivity (Maple 1979a, Perkins 1992), such as at the Singapore Zoo (Poole 1987), where allogrooming and social play among adult females was much higher than one would predict from behavior observed in the wild (but see also Markham 1990). The remarkable sociality of the primate order in general is the most relevant characteristic for their humane housing. This social tendency may be redirected toward animals of other species, including humans (Collazo 1989, Hediger 1964, Mason and Kenney 1974).

a. Social organization

The gregariousness of a primate in nature varies not only with its species, but may also vary with its age, sex, kinship to others, the season, the habitat, and the particular activity. The composition of a group that sleeps together is not necessarily the same as that of the foraging or breeding group (Cheney *et. al.* 1987, Jolly 1995, Rowe 1996). Group sizes can range from two, as in a monogamous pair of gibbons with no offspring, to 400, as in some hamadryas baboon troops (Rowe 1996). Bolivian squirrel monkeys live in large, but sexually segregated groups, enforced by the females, except during the breeding season (Williams and Abee 1988). Foraging associations between some primate species also occur and may provide a basis for mixed-species housing (Bernstein 1991, Bramblett 1989a, Thomas and Maruska 1996).

Jolly (1985) summarizes the breeding systems of many species. Monogamy, polygamy, polyandry, and multi-male, multi-female groups are all represented among the many primate species and those social structures are species specific. Some species can exhibit more than one breeding system, for example, many Callitrichidae can be either monogamous or polyandrous. Generally one male or multi-male groups are the rule among Old World Anthropoids; monogamy and polyandry, as well as multi-male, multi-female groups, are common in New World Anthropoids.

Close social bonds may exist between heterosexual breeding partners and/or between adult males, adult females, among juveniles, between parents and offspring, between infants and other kin, between non-kin. These patterns of bonding and association are also species specific and are often determined by degree of kinship (DeWaal 1993, Gouzoules and Gouzoules 1987). For many species, kinship appears to be the ultimate cause of social bonds between non-mated individuals in nature. But in captivity, if certain conditions are met and group formations are made with care, affiliative bonds can readily form between unrelated individuals that would not otherwise associate peacefully in nature (Gust *et. al.* 1996, Meshik 1994, Vermeer 1997, Williams and Abee 1988).

The generalized fear of strangeness or xenophobia that appears to characterize many primates accounts for the difficulties associated with socializing unfamiliar individuals together in captive settings (Bernstein 1991). Even relationships between primates in an established pair or group are not without stress and hostility, in the wild or in captivity. Primate societies are rarely composed of members of equal social rank, but rather consist of dominant and subordinate members. Some species tend to show strict and stable dominance hierarchies while others have more unstable or non-linear arrangements (Jolly 1995, Fragaszy 1994). Changes in group structure or dominance status are associated with physiologic evidence of stress, which may persist long after the event (C. L. Coe 1991, Ray and Sapolsky 1992, Van Schaik *et. al.* 1991).

In species such as guenons that normally live in groups consisting of one adult breeding male with several related females and immature offspring, two adult males are not likely to be compatible companions for each other in captivity (Cords 1987). But this does not mean that either male is unsuitable for social housing. It may simply be a matter of finding the right kind of social partner(s). Guenons are reportedly tolerant of social partners of other species (Bramblett 1989).

Patterns of emigration from the natal group and immigration or transfer into other groups is also species specific. Knowledge of these patterns is

essential for successfully forming pairs or groups in captivity, managing group sizes, and assuring the proper developmental environment for captive juveniles (Williams and Bernstein 1995). When it is necessary to remove individuals, it should be done in a way that minimizes disruption of stable social structures, and removals should approximate natural patterns of change to the extent practical (McGrew 1981).

In some species such as gelada baboons or gorillas, young males leaving their natal groups may travel alone for a while or may join together in bachelor groups. For a given individual in the wild, this arrangement is usually temporary, since the objective is to join a reproductive group (Jolly 1995). In captivity, squirrel monkeys, guerezas, lion-tailed macaques, and gorillas have been managed as bachelor groups (Harcourt 1988, Vermeer 1997, Watts and Meder 1996). In chimpanzees, young females normally emigrate from their natal groups and males form the cohesive core of societies (Goodall 1986). Chimpanzee males may also be kept in bachelor groups (Alford 1995).

b. Social signals

One of the most important primate behaviors associated with social living is the wealth of signals that communicate emotional states or other information between individuals. The signals may be visual, vocal, olfactory, or tactile. They can convey dominance, submission, intent to attack, anxiety, reconciliation, reassurance, alliance, sexual receptivity, a solicitation for grooming or play, a willingness to nurse, territorial boundaries, and so on (Estes 1991, DeWaal 1989, Rowe 1996, Zimmerman *et al*. 1980). Knowledge of these communicative and associated sensory abilities have led to various sensory enrichment ideas (Buchanan-Smith 1997, Shepherdson *et. al.* n.d.).

Visual signals include facial expressions, gestures, postures, and athletic displays of jumping, running, and object manipulation (Cheney *et. al.* 1989, Estes 1991, Goodall 1986, Zimmerman 1980). Vocal expressions can be context and gender specific (A. P. Clark and Wrangham 1994, Palombit 1992, Scott 1997). Prosimians and most New World Monkeys use odors to mark territory, indicate status, or compete with rivals (Jolly 1995, Ruiz 1993, Zimmerman *et. al.* 1980).

c. The importance of grooming

Grooming is the most important form of tactile communication and stimulation for primates (Olfert *et. al.* 1993). Social grooming can account for 10-13% of the daily activity budgets of rhesus macaques (Malik 1986). Chopra *et. al.* (1992) found that grooming was the most frequent social interaction in rhesus monkey troops in various habitats, generally beginning immediately after the first feeding period in the morning and continuing throughout the day. In capuchins *(Cebus spp.)* grooming is the primary activity during daytime rest (Robinson and Janson 1987). One grooming bout observed between a wild chimpanzee and her adult son lasted 2 hours and 45 minutes (Goodall 1986).

Grooming is the most critical activity in maintaining social bonds for most species (Prince *et. al.* 1989, Williams and Bernstein 1995). Jolly (1985) has called grooming "the social cement of primates from lemur to chimpanzee." Relaxed and affectionate grooming bouts between two primates are frequently seen by human care givers as an indication of successful affiliative bonding (Crockett *et. al.* 1997, Reinhardt *et. al.* 1995b). Grooming is not the only tactile interaction important for social cohesion and harmony: embracing, huddling, patting, kissing, and the tail-twining seen in titi monkey pairs are others (Cheney *et. al.* 1987, Jolly 1985).

2. Social Communication in Captivity

Communication between animals can be used by managers to recognize affiliative or stable bonds as well as aversion or impending aggression (Bernstein 1991, Rosenblum and Andrews 1995). Dominance relations can be established between laboratory macaques through visual signals between two individuals in adjacent cages and are an important tool for predicting successful pair introductions (Lynch 1998, Reinhardt 1995b).

It is therefore important that captive environments for primates allow for the adequate expression of social signals by the sender and reception by the receiver. Where postures and positions are part of the behavioral repertoire by which individuals normally establish or maintain social relationships, cages must supply enough room to safely express them. Other characteristics of the physical environment, such as furnishing and cage placement, must accommodate signaling. Threat signals can be a source of distress for recipients. In one case, a singly-caged male rhesus macaque persistently expressed abnormal behavior and severe anxiety when housed where he was in direct view of a dominant male. The situation was improved somewhat by moving the subordinate male's cage out of view of the other animal (Baer 1998a).

The expression of olfactory and tactile cues requires appropriate substrates for scent-marking and opportunities for contact, proximity, and avoidance. Cage boundaries do not stop olfactory signals. In common marmoset (*Callithrix jacchus)* colonies, olfactory and visual cues given by dominant females can suppress ovulation in subordinate females housed in separate cages in the same room (Tardif *et. al.* 1994). Because of the importance of scent-marking to New World species, it is highly recommended that sanitization of various surfaces and furniture within the cage be done sequentially, rather than all at once, so that a familiar territorial scent is always present (Buchanan-Smith 1997, NRC/ILAR 1998).

Whether a primate correctly uses and interprets social signals depends on its social experience and rearing history. A primate learns the customs of its own kind from adults or older peers during periods of early development (Fairbanks 1993, Fritz 1986, Jolly 1985). Young rhesus macaques with restricted social rearing may launch into "suicidal" attacks on mature adult males, apparently because the abnormally-reared animals are unable to recognize the danger (Mitchell *et. al.* 1966). A rhesus harem headed by a male reared in isolation had more problems with aggression and

wounding than harems led by males reared by their mothers or peers (L. Watson *et. al.* 1995). Bernstein (1991) suggests that lack of shared communication mechanisms might explain instances where groupings of animals of different species began without overt hostility but later deteriorated into violence.

3. Research Findings on Social Housing and PWB

Primates are clearly social beings and social housing is the most appropriate way to promote normal social behavior and meet social needs. However, there is no doubt that there are risks and negative impacts associated with both individual and social caging in captivity.

The relative benefits and costs to the animal of either alternative have been discussed extensively in primatological literature and are reviewed here. There is an emphasis on species used in laboratories, where single caging continues to be more common than in other types of facilities.

a. Detrimental effects of single-caging

Many authors have described the pronounced association between abnormal behaviors and/or physiological disturbance and single cage housing (Bayne *et. al.* 1991, Brent and Hughes 1997, Goosen 1988, Goosen *et. al.* 1986, Schapiro *et. al.* 1996a, Visalberghi and Anderson 1993, Watts and Meder 1996, Woolley 1997). In one study, chimpanzees that were moved from group housing to single caging exhibited increased stereotypical behaviors in the short term (Brent *et. al.* 1989). Individual caging of infants and juveniles impairs animals' social skills, makes them more difficult to socialize later in life, and may result in abnormal reaction to stimuli (Capitanio 1986, Fritz 1986, Louwerse *et. al.* 1997, Mason, W. A. 1991, Prince *et. al.* 1989, Young *et. al.* 1996). Walsch *et. al* . (1982) have stated that "even relatively complex laboratory environments, in the absence of opportunity for interaction with conspecifics, disrupt and seriously damage psychological processes in the chimpanzee".

b. Beneficial effects of social housing

Many beneficial effects of social housing are well documented. Social grouping reduced abnormal behavior in previously individually caged macaques and baboons at a pharmaceutical laboratory (Woolley 1997). Group-housed squirrel monkeys exhibited more normal behavior than individually-housed ones (Spring *et. al.* 1997). Social enrichment for young rhesus macaques both increased species-typical behavior and reduced abnormal behavior (Schapiro *et. al.* 1996a). The well-being of adult female rhesus macaques, based on behavior, was improved after a switch from single to pair housing; measures of physiology and reproduction did not indicate that the pairing caused significant stress (Eaton *et. al.* 1994). In juvenile squirrel monkeys, the presence of a peer mediated stress responses (stress vocalizations and plasma cortisol) to manual capture and exposure to a strange environment (Hennesy 1984). A familiar conspecific plus a familiar environment mediated the stress response to maternal separation (C. L. Coe *et. al.* 1987). Similar results have been obtained for pigtailed macaques and bonnet macaques (Laudenslager and Boccia 1996). In another study, cell-mediated immune function in pair-housed adult rhesus was superior to that of single-caged controls (Schapiro *et. al.* 1997b). Social companions lowered blood pressure in baboons (Coelho *et. al.* 1991), and pig-tailed macaques being groomed by conspecifics had reduced heart rates (Boccia 1989). Where nonhuman primates are subject to frequent manipulation and exposure to unfamiliar environmental stimuli, the presence of a compatible conspecific may be significant in helping them to cope with these realities of captive life (Gust *et. al.* 1994).

c. Avoiding potential detrimental effects of social housing

There have also been concerns over potential detrimental effects of pair or group caging versus individual caging. These effects can include social stress, competition for food, disease transmission, woundings, and the possible need for contraception. Gust *et. al.* (1996) found that cortisol levels were increased in pig-tailed macaques after group formation. Christopher Coe (1991) detected reduced cell-mediated immunity in geriatric rhesus monkeys when paired with juveniles, though such effects were not evident in the geriatrics' behavior. There is certainly also a risk of wounding during social caging, especially in reportedly "aggressive" species like macaques. However, pair housed rhesus at one facility required less veterinary treatment than rhesus in single or group caging (Schapiro and Bushong 1994). The conventional wisdom has been that species with this type of social organization are too difficult to pair or group in laboratories (Rhine and Cox 1989, Williams and Bernstein 1995). One resocialization of formerly single caged rhesus macaques resulted in aggression and increased stereotypies (Ljungberg *et. al.* 1997).

But there are also many instances of compatible pairs or groups of these species (Seelig 1998). Long periods of individual housing do not appear to reduce the need or desire for social contact (Taylor *et. al.* 1998). Animals that have been socially isolated have been successfully resocialized (Fritz 1989, Kessel and Brent 1997, Reinhardt 1994b). At one facility, adult male rhesus were paired with an 80% success rate, even though they had a history of being single-caged (Reinhardt 1994a).

Reinhardt *et. al.* (1995b) analyzed evidence for and against social housing of macaques in research facilities and concluded that the commonly given reasons for avoiding it were not supported by evidence. Even some of the infectious disease research commonly performed with chimpanzees does not appear to require single caging (Prince *et. al. 1989*). Visalberghi and Anderson (1993:8) have stated: "The gap between principles derivable from constantly updated knowledge on primates' psychological and physiological well-being and many existing regulations and practices is wide and unfortunate."

4. Management of Social Groups in Captivity

In creating appropriate social groupings in captivity, there are many factors to consider: Should animals be paired or in larger groups? What will be the group structure in terms of age and sex? What is the rearing history and personality of the candidates? How will group size be regulated? By what method will the group be formed and members added or removed artificially, if necessary? By what means will compatibility be determined? What equipment and enclosures will be needed and how will space be structured? How will humans fit into their social life, and will a behavioral conditioning program be implemented? How will the purpose and use of the animals, or their medical treatment, affect social stability? What will be done with socially incompetent individuals?

Many criteria for selecting partner candidates and methods of introduction and group formation have met with success and failure, perhaps even in the same setting. Many factors may impinge on the likelihood of success of any pairing or grouping, including individual personality (Reinhardt *et. al.* 1995b). Some grouping methods seem less prone to risk than others, and certain precautions seem well-advised.

Infants and juveniles of most species are easiest to introduce to established groups, to adults, or to each other. For animals like male macaques, an infant or juvenile can make good social partner (Fragaszy *et. al.* 1994, Reinhardt *et. al.* 1987, Schapiro *et. al.* 1994). All introductions should be closely monitored for as long as possible before leaving animals unattended, and there should be a plan for separating animals quickly if there is an attack. Since virtually any social change is a stressor, it is best that initial introductions occur at a time when other environmental factors are stable (Capitanio 1998). Beyond that, advice for pair or group formation among the major social types of primates varies. Different reports have yielded conflicting information on the role of prior familiarization, age differences, presence of the opposite sex, "neutral" cage environments, and other factors (Alford *et. al.* 1995, Bernstein 1991, Brent *et. al.* 1997, Crockett *et. al.* 1994, Reinhardt 1994a, Seelig 1998).

The method of introduction, as well as the rearing history, age, and sex of partners, may influence pairing success in macaques (Schapiro *et. al.* 1994). Crockett *et. al.* (1994) were able to compatibly establish only 6 of 15 attempted pairs of male cynomologous macaques (*Macaca cynomologus*) in a two week period. However, pairs were separated and re-paired daily. Higher rates of success in the same species and sex occurred at a facility where pairs were not continually re-separated (Lynch 1998). At this laboratory, 16 of 17 attempted male cynomologous pairs were established and remained compatible after one to two years. These researchers used a nine step partner evaluation and introduction technique that has been successful elsewhere in establishing long-term compatible pairs of adult male rhesus, adult female rhesus, adult male stump-tailed macaques and adult female stump-tailed macaques (Reinhardt *et. al.* 1995b). In Lynch's laboratory, an additional six pairs of male cynomologous were formed using an exercise cage (Lynch and Baker 1998). Similar techniques have been used to form compatible isosexual pairs of cynomologous macaques (Mack 1998) and to socialize pig-tailed and bonnet macaques (Taylor and Laudenslager 1998). At an animal sanctuary 18 former laboratory cynomologous macaques have been paired (Asvestas 1998).

Seelig (1998) contrasted the methods used in five studies on the pairing of adult male cynomologous macaques. The widely varying success rates in these studies suggest that adult male cynomologous macaques are more challenging to pair than other combinations of species and sexes. Where full-contact housing is not successful for these adult males, a safe alternative is adjacent caging with privacy panels and vertical bars that permit allo-grooming. In a test of one such design, all male-female and all female-female pairings were successful. Forty of 45 male-male pairs were successful, and nearly half of these successful pairs had not been compatible when previously housed together in one continuous enclosure (Crockett *et. al.* 1997). These cages can be used with partners of the opposite sex without resulting in unwanted pregnancies.

There are other reports of successful pairing or grouping of many species in pharmaceutical, toxicological, and other research settings: cynomologous macaques (Brinkman 1996, Buerge and Weber 1997, Heath 1989); rhesus macaques (*Macaca mulatta)* (Bowditch *et. al.* 1997, Buerge and Weber 1997, Fligiel and Reinhardt 1994, Louwerse *et. al.* 1997); pig tail macaques (*Macaca nemestrina*) (Gust *et. al.* 1996); rhesus macaques (Brown *et. al.* 1997); capuchins (*Cebus*) (Fragaszy *et. al.* 1994); chimpanzees *(Pan troglodytes)* (Alford 1995); squirrel monkeys (*Saimiri)* (Salzen 1989); bonnet macaques (*Macaca radiata)* (Taylor *et. al.* 1998).

Squirrel monkeys seem particularly well-suited to being kept in large groups, in a free-ranging room (King and Norwood 1989). An tame adult brown capuchin (*Capucinus apella*) who had formerly been a pet was successfully introduced to an existing group (Anderson *et. al.* 1991). Juvenile and adult female capuchins can be introduced to existing groups without great difficulty; males can also be integrated into groups that have no resident adult males (Fragaszy *et. al.* 1994).

For other descriptions of introduction techniques, see the following sources: Baer 1994, Byrum and St. Claire 1998, Cooper *et. al.* 1997, Kurth and Bryant 1998, Schapiro *et. al.* 1994, Reinhardt *et. al.* 1995b, Fritz 1994, Watts and Meder 1996, Ljungberg *et. al.* 1997, Morland *et. al.* 1992, Fragaszy 1994, Alford *et. al.* 1995. Behavioral conditioning (training) has been used to improve compatibility (Bloomsmith *et. al.* 1994).

5. Separations

Once animals have been compatibly paired or grouped, separating them is stressful. Any disruption of attachments will be stressful, whether it is separation from the mother, a sibling or nursery peer, a cage partner, or a room-mate in a separate cage (Capitanio 1998, Mendoza and Mason 1986, Prince *et. al.* 1989, Suomi *et. al.* 1975). Separations occur naturally in the wild, as part of normal weaning, death, and emigration. Stressful effects may be reduced in group-living species by the presence of group mates and/or minimizing other environmental changes (Coe *et. al.* 1987b, Gerber *et. al.* 1997, Reinhardt 1995b).

After pairing, the frequency and duration of unnecessary separation of an animal from its companion should be minimized (Olfert *et. al.* 1993). In the past, traditional laboratory settings made this nearly impossible. More recently, refinements in animal handling and restraint methods are making separations for husbandry, treatment, and experimental purposes increasingly unnecessary. Primate pairs have been trained to cooperate in a variety of clinical and husbandry procedures (Brown *et. al.* 1997, Gilbert and Wrenshall 1989, Reinhardt 1997d, Reinhardt *et. al.* 1995b, Turkkan 1989). Where separation is necessary, social partners should be able to maintain as much visual and auditory contact as possible (Lynch 1998, Reinhardt *et. al.* 1995b, Washburn and Rumbaugh 1991). It is also beneficial to prevent total separation by providing opportunities for tactile contact. If this cannot be done, providing items for tactile stimulation is the next best alternative (Lam *et. al.* 1991).

6. Choosing Between Pair and Group Housing

We have established that social housing is superior for most social primates, but should it be pair or group housing? In captivity, primates tend to be held as single animals, in pairs, or small social groups. Maintaining groups of three or more in captivity can be more difficult than maintaining pairs. Many of the references examining overt aggression in group housing situations involve groups of three or more in confined spaces (Bernstein 1991, Reinhardt 1991, Rhine and Cox 1989). Reinhardt *et. al.* (1995b) discusses why housing animals in pairs may be the best compromise between single and group caging for the majority of laboratory situations, even though the pair is not a species-typical social arrangement for most of the species commonly kept in laboratories.

For monogamous pair-bonding primates such as Aotus, Callicebus, and some Callitrichidae, only two adults will likely be tolerated, and these must usually be of opposite sexes (Baer 1994, NRC 1998).

Larger groups may be necessary for some species such as chimpanzees and squirrel monkeys (K. C. Baker 1996, Maclean *et. al*. 1987, Mendoza and Mason 1989, Olfert *et. al.* 1993, Prince *et. al.* 1989, Young *et. al.* 1996). K. C. Baker (1996) concludes that even one or two conspecifics are not sufficient to meet the extraordinary social needs of chimps in stimulus-restricted environments. Macaques, vervets, and squirrel monkeys have been successfully kept in medium-sized groups. So far, large social groups exist only at a few zoos and laboratory breeding colonies.

7. Social Adjustments and the Physical Environment

Social compatibility can be influenced by environmental structure and complexity (Chance *et. al.* 1983). Appropriate enclosure size, design, and furnishings can make attempts at social housing and the process of introduction more successful. In one group of chimps, aggressive behavior increased as enclosure space decreased (Howell *et. al.* 1993). Two unfamiliar individuals, at first pairing, may actually require more than twice the minimum space required by USDA for each individual alone because of the distance they feel they must maintain from each other. As previously discussed, there must also be room enough for appropriate social signals.

Physical features such as visual barriers, privacy panels, mesh dividers, multiple shifting points, escape routes, refuges, and perches have all been recommended to increase chances of successful pairing or grouping (Adang *et. al.* 1987, Aureli *et. al. 1997*, Bettinger *et. al.* 1994, Bramblett 1989a, Fouts 1989, Fritz 1986, Fritz 1989, Goosen *et. al.* 1984, Mendl and Newberry 1997, Prince *et. al.* 1989, Seier 1996, Watts and Meder 1996). Williams *et. al.* (1988) found that among mixed-sex group-housed squirrel monkeys, housed in cages with perches at multiple levels, males (which are subordinate to females) occupied perches below those preferred by females. Without a choice of perches, males were forced to stay on the floor. Mesh tunnels, connecting passages, coupled cages, and large exercise pens have been used to facilitate social introductions and periodic social contacts (Buchanan-Smith 1997, Field *et. al.* 1992, Lynch and Baker 1998, Marriott *et. al.* 1993). Primates in zoos need appropriate visual barriers or psychological distance from human visitors (Chamove *et. al.* 1988).

Food, water, shelter, and enrichment devices should be distributed to reduce hoarding (Lynch 1998). Foraging enrichments that disperse individuals and occupy their time can reduce tension and distract them from aggression (Boccia 1989). Behavior modification techniques, such as those used for most animal training, reduced social aggression in chimps (Bloomsmith *et. al.* 1994).

Nearly any two conspecifics might be housed together "compatibly" given just the right environment. For some individuals, this could entail huge, complex enclosures that contain a large inter-individual distance. Even two very compatible individuals may become aggressive towards one another if crowded into a barren space for a long period and subjected repeatedly to additional inescapable stress. These extreme hypothetical cases illustrate that social compatibility exists along a continuum that can vary with other factors. Animals should not be judged unsocializable on the basis of their behavior under conditions approaching the latter example. Rather, an appropriate physical setting must be provided to accommodate social living.

There is no doubt that successful pair or group housing of primates requires the proper caging and equipment. In order to maximize the potential psychological benefits of social housing and minimize the risks to animal well-being, individuals must have the right kind of space for social adjustments. In addition to the enclosure dimensions that accommodate interaction, the space must be shaped and furnished so that postural and other social signals can be used by the animals to maintain relationships, as in the wild. Caging systems need to be adapted to suit appropriate social grouping rather than the reverse. Resources such as food and water, resting sites, and enrichment devices also need to be chosen and distributed to respect mechanisms for maintaining social relationships.

8. Effects of Human Interaction

Positive interaction with humans can improve the social environment for captive primates (Bayne *et. al.* 1993b, Bloomsmith *et. al.* 1997, K. C. Baker 1997b). Although it should not replace the conspecific social interaction intended by the regulations, positive interaction with humans is valuable in two situations:

- Where conspecific socialization is impossible or detrimental to the animal. In the absence of the mother, a human attachment figure can moderate young chimpanzees' neophobia and enhance coping and exploration responses (Miller *et. al.* 1986). Nonhuman species, such as dogs, may also provide companionship. Another study of infant chimps found that dogs were even more useful enrichment than humans (Pazol and Bloomsmith 1993).

- Where forced contact by human facility personnel is a necessary part of the animals' daily life. Some level of socialization with humans is likely to be necessary to improve psychological well-being because the animals cannot escape contact. Without some socialization to humans, this contact is an environmental stressor over which the animal has no control (Heath 1989, Olfert *et. al.* 1993, Van Vlissingen 1997,)

Many regard a positive, relaxed relationship with human keepers as one of the most important components of captive primate well-being (Poole 1997b, Reinhardt 1997e). Reinhardt warns of potential problems with keepers who appear dominating and intimidating. Those who work with primates must be knowledgeable about primate gestures and vocalizations to avoid inadvertently threatening or stressing primates with their own movements and body language (National Research Council, Institute for Laboratory Animal Research 1998).

The activities and presence of humans may also have significant negative effects on primates. At three chimpanzee breeding facilities, births occurred significantly more often during periods of low human activity (at night and on weekends). This was attributed to the greater privacy and reduced stress during such times (Alford *et. al.* 1992). Line *et. al.* (1989b) found that even routine events like cage cleaning caused elevated heart rates for several hours. On the other hand, Line (1995) also found in another project that study observers had no significant effect on most primate behaviors and that "a period of habituation to an observer...is not always necessary". Thus, unfamiliar humans who must enter a primate area occasionally to make observations, may be able to avoid influencing behavior unduly just by remaining calm and avoiding threatening actions, such as direct stares.

At many facilities, programs of animal training using positive reinforcement techniques have been successful in reducing the stress that normally accompanies manipulations by humans. The cognitive stimulation and pleasurable interaction with humans that such training entails may in itself be enriching (Laule and Desmond 1998). Reinhardt (1997d) collected 46 published reports on the training of primates to cooperate with clinical and husbandry procedures such as shifting from cage to cage, capture, venipuncture, urine collection, and drug administration. Traditional stressful methods of manual restraint and handling are often unnecessary (Reinhardt *et. al.* 1995a). In only 21 days, Drea (1998) trained a colony of 55 rhesus macaques to repeatedly divide themselves into two groups for a social behavior study. Scott (1990) criticizes training methods using food deprivation. Gifted animal trainers in the film and animal exhibit industry have successfully trained many animals to consistently perform complex tasks, without resorting to water or food deprivation.

9. Periodic or Partial Contact

The social needs of most primates cannot be completely met by single housing. As previously discussed, social primates are very much physical contact animals. Continuous full contact housing, in pairs or appropriately structured social groups allows primates to express sophisticated social adaptations (Jane Goodall Institute 1988, Prince *et. al.* 1989, Visalberghi and Anderson 1993). Walsch *et. al.* (1982) concluded that chimpanzees' "opportunities for visual and auditory contact with conspecifics, in the absence of tactile contact, do not appear to significantly reduce levels of disturbance." In situations where continuous social housing is not appropriate, due to the health or personality of the individual animal or to research protocol requirements, caging allowing periodic full contact or even partial contact with conspecifics can be justified with appropriate supporting evidence (Bayne 1991, Taylor *et. al.* 1998). The more socially restrictive the housing arrangement is, the more rigorously it must be justified.

This does not mean that every individual primate must be forced into social contact. There will be situations where single housing would still be preferable to contact with unsuitable conspecifics. For example, an adult male owl monkey would be more appropriately housed alone, than with another adult male, if that is the only social partner available (Baer 1994).

10. Summary

Companions do not just meet innate social needs in primates. A compatible companion supplies environmental novelty, multi-sensory stimulation, something to manipulate, and opportunities for cognitive challenge and control. Appropriate social enhancement is one of the most versatile and option-laden forms of enhancement we can provide.

B. Social Needs of Infants

Psychological well-being in primates depends on appropriate infant development. Reproductive success (including reproductive behaviors, fertility, prenatal adequacy, parturition, and parental care) is generally considered to be the strongest indicator of psychological well-being in captive nonhuman primates (Novak and Suomi 1991). It is necessary for primate individuals to learn appropriate behaviors to allow them to function in their captive environments. Experiencing effective parenting at an early developmental stage allows the young primate the opportunity to grow into a healthy and responsive adult. The young primate ideally will translate positive early experiences into subsequent social skills, including parenting (Suomi 1986.)

1. Normal Behavioral Development During Infancy

Developmental sequences in young primates may be characterized in the following manner. The neonatal primate is termed an infant until the time it can survive its mother's death. This period encompasses weaning. Infancy is followed by the juvenile stage, which takes the young primate up to the onset of puberty. After puberty, but before reproduction, the primate is considered an adolescent. It must be noted that these definitions are imprecise and are not used consistently across species (Walters 1987).

Infancy in primates is characterized by a variable period of helplessness and dependency. The mother provides nourishment, transportation, protection, and education. The newborn's survival is critically dependent on establishing and maintaining a satisfactory relationship with its mother (W. A. Mason 1986). It must also be recognized, the infant is an active participant in its own postnatal development. W. A. Mason (1971) characterizes the developmental trends in infant primates as a balance between two functional systems: filial ("mother-directed") and exploitative ("other-directed"). Both functional systems exist concurrently in varying degrees throughout the life of the developing primate. As expected, mother-directed behaviors predominate in the neonate: clinging, rooting, and sucking. These behaviors reduce infant arousal and anxiety. This, in turn, enhances the formation of filial attachment. A shift toward exploitative behaviors, such as investigation and play, evolves as the infant develops and interacts with its environment.

Weaning commences as the infant matures. The weaning process consists of two concurrent processes: behavioral weaning and nutritional weaning. Nutritional weaning is completed at the time the infant is no longer dependent on the mother for total provision of food. As the infant grows, the diet is increasingly supplemented with other foods eaten by members of the same species, including insects, fruit, and vegetation. Typically this is a gradual process. Behavioral weaning extends beyond the conclusion of nutritional weaning. This transition encompasses the period during which the infant may nurse, not primarily to obtain food, but to obtain comfort and reassurance during times of stress (Byrne and Suomi 1995, Goodall 1986, Van Roosmalen and Klein 1988). The infant will seek to prolong this period as a means of maintaining the mother-infant bond.

Harvey *et. al.* (1987) have noted the weaning age in primates is strongly correlated with neonatal body weight. Ranges for weaning ages extend from the relatively brief (2 months for some callitrichids) to very long (52 months for some gorillas).

Continuing development in the young primate is influenced by a variety of factors. The age at which an infant will attain independence varies by species. Social structure and group dynamics may play a role in development, depending on species and situation (Milton 1993, Nash 1993, Watts and Pusey 1993). In some species, the presence of alloparents and/or peer conspecifics is essential to promote appropriate development (Worlein and Sackett 1997, Young *et. al.* 1996). Resource availability, such as proper nutrition, adequate usable space, and privacy, may have profound impact on development. The ability to play with others, including parent(s), conspecific peers, or surrogates, enhances the acquisition of locomotor and social skills (Fagen 1993, Fairbanks 1993, Govindarajulu *et. al.* 1993). Individual variations within a species must also be considered: a confident, secure animal may show independent characteristics earlier than a weak, submissive one.

2. Research Findings Related to Development in Captivity

The optimal situation in which any primate should develop is one that permits the infant to remain with its biologic mother through weaning in the company of a species-normal social group (Pazol and Bloomsmith 1993, W. A. Mason 1991,). International Primatological Society (1993) guidelines recommend the young of most species should be allowed to remain in contact with the mother until at least 12-18 months old. Primate Vaccine Evaluation Network (PVEN) guidelines state infants should not be weaned before 6 months and recommend weaning at 12 months old (Poole and Thomas 1995).

Early studies by Harlow and Harlow (1965, 1972) tested the importance of affectional systems in the developing primate by subjecting newborn rhesus macaques to an array of deprivation. Reared in total or partial social isolation, these infant monkeys could not function socially as they matured. They demonstrated inadequate play, social behaviors, and, later, abnormal sexual and maternal behaviors. Other studies by Harlow *et. al.* (1963) showed that motherless infant rhesus monkeys could be reared with more success in peer groups. These monkeys bonded strongly with each other, as manifested by increased clinging behavior. When the clinging behavior was discouraged, however, the infants exhibited play behaviors which approximated adequate social adjustments. Surrogate studies by Harlow revealed infants separated from their mothers and reared in the presence of various surrogates (inanimate models) exhibited varying degrees of disturbed behaviors. However the degree to which these youngsters displayed aberrant behaviors was less than it was for maternally-deprived infants reared without any surrogate interaction. Other surrogate studies have evaluated the use of simple objects such as shaped wire forms, the complex interactions with conspecific peers in a nursery environment, and

interactions with unrelated adults or phylogenetically remote surrogates such as dogs (Pazol and Bloomsmith 1993, Rumbaugh *et. al.* 1989, W. A. Mason and Kenney 1974, W. A. Mason and Capitanio 1988). In general, these studies found the closer the surrogate approaches species-specific maternal nurturing behaviors, the better the infant's chances are to develop adequate and appropriate behavior. No combination of maternal, surrogate, and/or peer contact is quite as effective as the species-typical, mother-peer group in producing completely normal animals. However, for rhesus monkeys, surrogate rearing with daily, but not continuous, contact appears to be the best approximation among the commonly compared regimens (Bayne and Novak 1998, NRC/ILAR 1998).

The response of the infant nonhuman primate to the loss of the mother-figure has been the focus of considerable research effort. These inquiries have sought to elucidate the dynamics of the mother-infant relationship. For the infant, maternal separation or loss is accompanied by a complex series of behavioral and physiological changes. Initially, an agitation/protest phase is observed, characterized by increased locomotion, distress vocalizations, and oral and ingestive behaviors. This phase is followed by a depressive/despair phase, in which the infant becomes increasingly withdrawn and despondent, manifesting reduced locomotion, slouched postures, and diminished interest in play activity. The degree to which an individual infant will exhibit these phases is influenced by a variety of factors: species, age, familiarity with the environment, presence or absence of alloparenting or other social support figures, and intra specific individual variations (Mineka and Suomi 1978, Worlein and Sackett 1997).

In many species, a history of nursery rearing is correlated with various abnormal behaviors in juveniles and adults. These include self-aggression, self-clasping, bizarre postures, rocking, regurgitation with reingestion, locomotor stereotypies, and others (Capitanio 1986, Gould and Bres 1986, Marriner and Drickamer 1994, Platt *et. al.* 1996). In chimpanzees, it is associated especially with body-rocking and self-clasping (Walsch *et. al.* 1982). Spijkerman *et. al.* (1994) found that of various rearing conditions, only rearing by the chimpanzee mother in the presence of peers did not result in development of rocking behaviors. Others found neither human contact nor peer contact were as effective as dogs in mitigating body rocking (Pazol and Bloomsmith 1993).

Infant physiological parameters are also profoundly affected by the disruption of the mother-infant bond. Studies of separated infant squirrel monkeys by C. L. Coe *et. al.* (1985) demonstrated changes in the level of circulating complement proteins and immunoglobulins and decrease in the capacity to mount an antibody response to an antigenic challenge. These findings are supported in other primate species: titi monkeys (Mendoza 1991) and bonnet and pig-tailed macaques (Laudenslager *et. al.* 1990). a study comparing pig-tailed macaques remaining with their mothers for the first 1.5 years of life to pig-tailed macaques separated from their mothers for as little as two weeks during the first year of life showed an association between separation and deficient immune responses in adulthood (Laudenslager *et. al.* 1985). The detrimental immunologic effects of maternal separation in primates can be buffered by allowing the infant to remain in the home cage and providing a familiar companion (C. L. Coe *et. al.* 1987a, Laudenslager and Boccia 1996). Disruption of the maternal-infant bond decreases heart and body temperature, as well as disturbs sleep patterns and EEG activity (Reite *et. al.* 1981). For reviews of the immunologic effects of maternal separation, see C. L. Coe (1993) and Capitanio (1998).

Research efforts have provided much information about negative effects on developmental processes, especially detrimental effects of isolation and early maternal separation. For many species we have an idea of what constitutes lack of well-being. (See Fouts *et. al.* 1989). It is much more difficult to quantify the positive side of well-being. Psychological well-being is not merely the absence of behavioral pathology and abnormality, however defined. It is something positive. But what? We have gained some insight into what situations to avoid when raising primates, but are only beginning to understand the components of a beneficial, species-appropriate environment. Optimal, as opposed to merely adequate, social and nonsocial infant development, is still to be defined.

3. Planning Appropriate Infant Development

A plan to enhance appropriate infant development within a primate population must address many factors. Physical environment is an obvious starting point. First, the plan must ensure that there is adequate space to express species-typical behavior. Both floor space and vertical space must be considered. Increased cage complexities (for example, ropes, swings, and shelves) allow for expression of species-typical locomotor activity and provide opportunities for play. Nesting materials, visual barriers, and refuges can add comfort to an enclosure. Some degree of control over their environment can offset stress in many individuals (Mineka *et. al.* 1986). Provision of manipulanda and the ability to move freely within the existing environment can ameliorate an animal's sense of helplessness and also decrease the level of frustration inherent in some types of captivity.

Social factors are also essential considerations in planning appropriate infant development. Family history, social groupings, age/sex mix, social rankings, individual personality and temperament play important roles, in addition to intrinsic species variations. Witnessing good mothering first hand allows females to observe and learn appropriate nurturing behaviors that they may later apply to their own infants (Miller-Schroeder and Patterson 1989).

To summarize, in most situations, the developing infant's optimal captive environment approximates what it would encounter in the wild, if the natural habitat were undisturbed and risk free. Expression of species-typical behaviors among members of the natal group permits the young primate to learn its role within the culture of its species community. When this structure is provided, infant development can flourish.

Although we have stressed the importance of not disrupting the bond between the infant and its parents or natal group, there are situations in which allowing the infant to remain may also be a source of problems. Cases of infanticide, parental neglect, and abuse of offspring have been noted in

both wild and captive environments. Aggression directed toward infants may be perpetrated by family members or unrelated members of the troupe. In captivity, this situation may necessitate removal of the infant from the hostile environment for its own safety. The decision to separate mother and infant introduces a constellation of factors to consider, including: species; health status; age and level of development and independence; availability of foster or surrogate care givers or peer groups; and the feasibility of later re-introductions.

C. Structure and Substrate

The social, developmental, and physical environment are interdependent in enhancing psychological well-being. The most basic components of the physical or inanimate environment are the enclosure structure (its size, shape, and design) and the substrates within it (J. Coe 1989, Maple and Perkins 1996, Poole 1991b). Although the term "substrate" commonly refers to the "base on which an organism lives" and would include flooring, turf, sand, soil, and bedding materials, in this section we include furnishings, perches, swings, ropes, ledges, nest boxes, barrels, culverts, and water features as well. These components should combine to create opportunities for species-typical resting, exploration, play, and foraging, as well as social interaction and adjustments (Prince *et. al.* 1989, Schapiro *et. al.* 1991, Thompson 1996). The enclosure should allow normal postures and a range of locomotion (Buchanan-Smith 1997, Dahl 1989, EEC 1986, Home Office 1989, International Primatological Society 1993, Marriott *et. al.* 1993, Olfert *et. al.* 1993, Poole 1991b, Poole and Thomas 1995, Poole *et. al.* 1994, Reinhardt 1997b, Snowdon and Savage 1989, Whitney and Wickings 1987).

In order to accommodate species-typical behavior, the enclosure must have adequate space. Use of legal cage size will not always meet an animal's behavioral requirements (NRC/ILAR 1998:18).

Adequate space is not just a question of numeric dimensions or total volume, but also one of shape and design. The space must be structured to be useable and species appropriate. This can be achieved through a variety of furnishings, projections, contours and floor coverings (Chamove and Anderson 1989, Maple and Perkins 1996, NRC/ILAR 1998, Poole 1991b, Schapiro *et. al.* 1991).

1. Resting Behavior

Primates display a variety of different comfort postures during resting and sleeping similar to those of other animals and humans: lying down; sprawling out prone, sternally or laterally; sitting upright; and crouching (Fleagle 1998, McGraw 1998). Vertical clinging is a normal resting, feeding and vigilance posture for many nocturnal prosimians, tarsiers, and callitrichids (Fleagle 1998). There must be something in the cage to which these animals may cling. Squirrel monkeys sleep hunched with their tails curled between their legs and up over their shoulders (Baldwin 1985). According to Abee (1985), large diameter tubular perches provide comfortable, contoured, and stable resting surfaces for squirrel monkeys and prevent the development of pressure sores at the base of the tail associated with the use of flat shelves or boards. Many prosimians, callitrichids, and owl monkeys use nests or cavities for sleeping (Rowe 1996).

In nature, great apes build night and day nests of soft materials. They appear to be painstakingly constructed for comfort (Fruth and Hohmann 1996, Maple and Perkins 1996, Van Lawick-Goodall 1968). While orangutans build their nests only in trees, chimpanzees, bonobos, and gorillas also build them on the ground (Tuttle 1986). Chimpanzee night nests are generally more elaborate than those constructed for day time naps (Van Lawick-Goodall 1968). Chimpanzee nest building skill appears to be learned from elders, with first attempts at eight months of age (Fruth and Hohmann 1994). Human-raised, captive chimpanzees removed from their mothers at birth were unable to construct good nests in adolescence or adult-hood, although some made rudimentary efforts and all manipulated the materials (Bernstein 1962). Suitable materials to facilitate development and expression of nest building include both artificial materials, such as blankets and shredded paper, as well as more naturalistic materials. Even chimps with no prior exposure to nest-construction benefit from these materials as manipulable items (Jane Goodall Institute 1988, K.C. Baker 1997a). Some ape breeding colonies and sanctuaries have provided chimpanzees with elevated "tire hammocks" (tires chained together in clusters), their contour and shape mimicking an arboreal nest.

2. Postures and Tail Positions

In designing enclosures for primates with long tails, one must take into account the position, angle and length of the tail so that it may be unobstructed and held comfortably in a normal manner (NRC/ILAR 1998). Goosen *et. al.* (1984) recommend that for long-tailed macaques, shelves should not be flush against a wall but should have a space between the edge and the wall through which the tail may hang. Poole (1991b) and Reinhardt *et. al.* (1996) demonstrate that many of the standard legal-sized laboratory cages for adult long-tailed macaques, including those given in the weight-based table of the minimum standards under the Animal Welfare Act, are not tall enough to permit a normal perching posture. Either the animal's head will be obstructed or its tail must be held up to avoid dragging in the waste pan. Cages of this height are inadequate for the "normal postural adjustments" and certainly for the "normal postural adjustments with adequate freedom of movement" required by USDA regulations in 9 CFR Section 3.80(a)(2)(xi). Species with certain anatomical features "might require a taller cage than other species of the same body weight." (NRC/ILAR 1998:26)

As previously discussed, a variety of postures, including tail positions, may be used in social adjustments. An enclosure should have proper dimensions to allow this. Vervets may hold their tails straight out from the body, more than doubling their effective body length while quadrupedal (Estes 1991). New World species use their prehensile tails as a fifth limb (Fleagle 1998). Tail-suspension postures are used in feeding and

exploration and for locomotion (Gebo 1992). Prehensile or non-prehensile tails may also be used for support or counterbalance (Baldwin 1985, Fleagle 1998). The Canadian Council on Animal Care (CCAC) Guidelines specify that to engage in normal postures, New World primates with prehensile tails should be provided with linear vertical space about four times the length of their body (Olfert *et. al.* 1993).

All of the apes use their arms and/or feet for suspensory postures. In chimpanzees and gorillas these are more commonly observed in juveniles than in adults (Baldwin 1985, Goodall 1986, Tuttle 1986). An enclosure without properly placed, suitable structures, like bars or hand-holds, cannot enable such postures (NRC/ILAR Report:1998). Bipedal postures, with or without suspensory or tail support, are in the repertoires of many species, including vervets (Estes 1991), spider monkeys (Fleagle 1998), squirrel monkeys (Baldwin 1985), bonobos, and chimpanzees (Tuttle 1986).

3. Locomotion

Locomotor styles vary among taxonomic groups, and most primates exhibit many types of locomotion. Brachiation and other similar forms of suspensory locomotion are seen in the Hylobatidae (gibbons), Atelinae (spider monkeys and wooley monkeys) (Fleagle 1998, Rowe 1996), some colobines (leaf-eating monkeys) (Rowe 1996), and all the great apes (Doran 1996, Estes 1991, Goodall 1986, Tuttle 1986). All primates are climbers, even those that are more terrestrial than arboreal (Chivers 1991, Estes 1991). Terrestrial knuckle walking is specific to gorillas, chimpanzees, and bonobos (Estes 1991). Orangutans walk on the sides of their curled fists (Chivers 1991, Rowe 1996, Tuttle 1986). Floor surfaces for apes in captivity should reflect consideration for comfortable knuckle- or fist-walking.

Ripley (1967) points out that simply classifying a species' locomotor style based on whatever mode that species uses most often does not tell enough about the overall locomotor abilities and patterns of that species. Although rhesus macaques are often simply described as quadrupedal, Dunbar (1989) observed walking, galloping, leaping, climbing, swimming, and even suspension in a free-ranging colony of captive rhesus macaques. The most common running gait was the gallop. Quadrupedal walking and running is exhibited by most primates, either on the ground or in trees. The substrates on which locomotion is most likely to occur differ among species and age classes (Fleagle 1998, Tuttle 1986). Stride lengths of primates are longer than those of most mammals (Reynolds 1987). Some primates are good swimmers, including long-tailed macaques (Rowe 1996), rhesus (Dunbar 1989), and vervets (Estes 1991). This has been put to good use as an enrichment choice for long-tailed macaques in a Canadian toxicology laboratory (Gilbert and Wrenshall 1989).

Leaping is part of the locomotor repertoire of many primates (Fleagle 1998). Callitrichids, colobines and most prosimians are excellent leapers (Estes 1991, Fleagle 1998). Tarsiers leap lengths of three meters (about eight times their body length) from vertical clinging positions. *Presbytis entellis*, the Hanuman langur, routinely leaps horizontal distances of 12 to 15 feet in trees, and occasionally 35 to 40 feet (Ripley 1967). Given the opportunity, the long-tailed macaque will leap 2.2 meters (Cant 1988). Chimps will leap 10 meters in trees (Estes 1991). In one field study of white-throated capuchins (*Cebus capucinus)*, leaping was 15% of the locomotor time budget, and nearly all leaps were of 1 to 4 body lengths and occasionally seven body lengths. Rarely did they leap less than one body length (Gebo 1992) .

Squirrel monkeys have been described as "incessantly active and manipulative" and showing a "rapid tempo of motor activity"; a study of their movements in a large enclosure showed they traveled over one kilometer per hourly observation session (Fragaszy 1985). In the wild, over 40% of their travel is through leaping, 11% of their locomotion during foraging is leaping (Fleagle 1981). They make frequent leaps of one to two meters in horizontal distance, and sometimes up to seven, with an 8 to 13 meter drop (Baldwin 1985). Several authors have pointed out these forms of normal locomotion are impossible for most primates to execute in standard enclosures of minimum size (Buchanan-Smith 1997, Marriott *et. al.* 1993, Snowdon and Savage 1989). King and Norwood state (1989:104) that for squirrel monkeys in such cages the "opportunity for leaping and sustained quadrupedal locomotion is virtually eliminated."

Similarly, Kessel and Brent (1995a) have pointed out that baboons do not have room to execute normal locomotion and much other species-typical activity in enclosures of the minimum size. A number of facilities have implemented programs of periodically releasing various species of primates into exercise areas to compensate for this.[(4)] The NRC Report (1998) encourages the use of exercise areas. Other facilities have enlarged the home enclosure with various expansions and attachments.[(5)] Many of these facilities reported that the exercise areas also served as areas of social contact. Seier and de Lange (1996) found weekly release of vervets into a mobile exercise cage allowed animals to engage in locomotor behavior and socialization not possible in their standard cages and allowed for better assessment of their motor function. King and Norwood (1989) describe how a whole room can easily become an enclosure for a group of squirrel monkeys.

4. Research Findings Related to Enclosure Size and Well-Being

We are not proposing to make any changes in existing cage space requirements already stipulated in the regulations. The body of professional literature relating to psychological well-being of primates is replete with discussions of the possible effects of this environmental factor, especially in combination with other methods of enrichment. Investigating the effects of dimensional space on primate welfare has been controversial and the results equivocal. Kessel and Brent (1995a) and Reinhardt *et. al.* (1996) summarize and critique many such studies. [See also Crockett and Bowden (1994:30), Fouts *et. al.* (1989:381), and Poole and Hubrecht (1994: 51), and Whitney and Wickings (1987:604) for other comments.] Most of these experiments have examined the effects of floor space or volume on physiologic and behavioral measures. The results of most of these were confounded with the effects of social condition (either social restriction or social enhancement), the presence or absence of other enrichment, or rearing history. As both Kessel and Brent (1995a) and Reinhardt (1996) argue, test conditions using barren cages with an absence of adequate

enrichment should be viewed as testing under abnormal conditions. They maintain that conclusions about the value of cage size for PWB should only be based on test conditions with otherwise adequate enrichment.

Long-tailed macaques in larger cages had a significantly higher successful pregnancy rate than those in cages with about one quarter of the volume (Boot *et. al.* 1985). Faucheaux *et. al.* (1978) compared effects of enclosure size, rearing history and social housing condition on growth and development of stump-tailed macaques and found animals kept in the smallest cage condition (0.64 square meters by 0.6 meters tall) were lighter and smaller, with noticeable muscle atrophy, than those kept in larger space conditions (23.5 square meters or 450 square meters). Turnquist (1983, 1985) found that housing patas monkeys in small cages had detrimental effects on joint mobility, which could be reversed by release into free-range habitats.

Positive behavioral effects have resulted from exposure to larger and more enriched environments in numerous studies.[(6)] Many of these involved release into an exercise space or activity cage, while others involved transfer to an enlarged primary enclosure or habitat. A study of common marmoset pairs using five levels of cage size and complexity showed stereotypies were displayed only in smaller cages and levels of aggression and startle response rates were higher in the small cages (Kitchen and Martin 1996).

Conversely, a number of other studies did not demonstrate beneficial effects on behavior and physiology from larger cages (Bayne and McCully 1989, Crockett and Bowden 1994, Crockett *et. al.* 1994, Goosen 1988, Line *et. al.* 1991a, Wilson 1972). Many authors concluded that the value of enclosure space is more dependent on its overall quality than on its quantity alone (Clarke *et. al.* 1982, Erwin 1991, Wilson 1982). Doyle *et. al.* (1996) expanded baboon cages with an attachment which enabled them to equip the cages with enrichment options that could not fit into the original cages. Kessel and Brent (1995a) made a similar point about the need for enclosures to be able to accommodate enrichment items of a size and type appropriate to the species.

5. Special Needs of Older Infants and Juveniles

We must also take into account the special structural needs of older infants and juveniles. The frequency with which juveniles use certain locomotion styles may differ from that of adults of the same species. Young gorillas and chimps engage in more suspensory behavior than adults. In a free-ranging colony of rhesus macaques, arboreal locomotion, occurring primarily during play, was more common among juveniles than among adults (Dunbar 1989). As with social skills, primates must learn motor skills and coordination as infants and juveniles (Fagen 1993, Govindarajulu *et. al.* 1993, O'Neill 1989). Whether particular sensory and motor skills have "critical " periods during development, as with social skills, is unknown.

According to Dunbar (1989:85), the wider ranges of locomotor behavior practiced by older infants and juveniles "provide the greatest opportunity for developing strength, balance, and coordination." In Turnquist's studies (1983, 1985), patas monkeys living in small (30" by 30") cages for five years, developed abnormal joint mobility. The effect was most pronounced among those animals that had begun living in these cages during the first 18 months of their life. The author concluded that "animals born and reared in cages never develop proper muscle tone."

Play is important for young primates (Fagen 1993, O'Neill *et. al.* 1990, Thompson 1996). Pereira *et. al.* (1989b) suggest that the expression of play behavior should be an index of well-being. "Locomotor play is far more vigorous than any normal locomotion" (Jolly 1985:402). Thompson (1996:365) states, "All captive immature animals should be provided with enough space to engage in vigorous locomotor play..." Goosen *et. al.* (1984) maintain that because young primates have a greater need for exercise they should be provided with the same interior cage height as adults of their species.

6. Designing for Arboreality

The most salient factor in structuring a captive primate's environment is the tendency to use vertical space. Primates will make ready use of vertical space and structures such as trees, ropes, cliffs, temple walls, poles, jungle gyms, and enclosure wall mesh (Bayne *et. al.* 1992a, Bennett and Davis 1989, Burt and Plant 1990, Eichberg *et. al.* 1991, Rowe 1996, Shimoji *et. al.* 1993, Suarez 1995). Providing opportunities to fully utilize the vertical dimension is one of the most frequent recommendations for environmental structure made by experts (Abee 1985, Buchanan-Smith 1997, Dukelow and Asakawa 1987, International Primatological Society 1993, Maple and Perkins 1996, Olfert *et. al.* 1993, Poole and Thomas 1995, Poole *et. al.* 1994, Reinhardt *et. al.* 1996, Queyras *et. al.* 1997).

Primates' preferences for the location and position of structures within their enclosures relate to their arboreal habits. Goff *et. al.* (1994) and Traylor-Holzer and Fritz (1985) found chimpanzees used upper levels of enclosures and perimeter areas the most. As previously stated, for groups of Bolivian squirrel monkeys in large enclosures, dominant individuals (females) took the highest available perches and less dominant ones (males) took lower perches (Williams *et. al.* 1988). Woodbeck and Reinhardt (1991) found that rhesus macaques in lower-row laboratory cages used their perches 24.7% more often than those in upper row cages. S. Watson and Shively (1996) observed 12 long-tailed macaques and found that animals in taller cages spent more time in the top third of the cage and exhibited self-directed stereotypies less often than those in shorter cages. Similar preferences for the upper parts of a cage have been displayed by tamarins (Caine *et. al.* 1992) and guenons (Bennett and Davis 1989). The International Primatological Society (IPS) Guidelines (1993) recommend that primates be able to "perch above human eye level." Double-stacked caging systems may force lower-row animals to remain below human eye level (NRC/ILAR 1998).

Primates display "vertical flight reaction". All animals display a minimum "flight distance" through which they will retreat from fear-inducing stimuli (Hediger 1964). Primates generally execute this in the vertical direction when available (Chopra *et. al.* 1992). Primates will be stressed if unable to retreat to this distance from frightening stimuli (Burt and Plant 1990, King and Norwood 1989, Whitney and Wickings 1987). Maple (1979) and Hediger (1964) suggested that enclosure dimensions should be sufficient to contain the normal flight distance. The exact distances will vary depending on the individual and the nature of the threat or stimulus. The 36 to 40 inches of retreat available in most minimum-sized cages for macaques will need to be carefully evaluated. Applebee *et. al.* (1991) designed an enclosure for laboratory stump-tailed macaques that is both tall and deep. However, enclosures should permit humans to capture their inhabitants when necessary. In modest-sized cages that problem can be solved through cage squeeze-back and squeeze-front mechanisms or pole-and-collar restraint systems. In very tall cages, accessibility of animals can be ensured with horizontal dividers and/or animal training (Applebee *et. al.* 1991, Burt and Plant 1990, Reinhardt *et. al.* 1995a). Adequate distances for normal flight response and proper, nonstressful capture and restraint are not mutually exclusive. A primate will become less fearful and more sociable (or "tame") towards its care givers as a result of positive human interaction, and its flight distance will decrease (Heidiger 1968).

For primates on public display, there is no reason not to maintain long distances between the viewing public and the primate. Maple (1979) suggests at least 20 feet of separation in such habitats. In one study, zoo visitors increased aggression and decreased affiliative social behavior in primate groups; the effect was more pronounced for arboreal species (Chamove *et. al.* 1988).

7. Designing Enclosure Furnishings

Perches, shelves, ladders, swings, ropes, barrels, boxes, and other structures can be made of many materials. These can be used for resting, retreating, playing, or staying dry. Wood, plastic, and fiber have the advantage of being non-thermoconductive, which is helpful outdoors on days with extreme temperatures. Cargo nets and large-gauge wire platform baskets are popular in ape enclosures at zoos. Schmidt *et. al.* (1989) and D. Watson (1991) explain methods of equipping standard laboratory cages with perches without interfering with squeeze back mechanisms. Providing perches may be the most inexpensive way to keep primates clean and dry during cage cleaning.

Izard (1991) describes how enclosures for various prosimians were furnished with natural and artificial materials of various sizes and arrangements suited to the species' anatomical characteristics and locomotor and social behavior. This created a network of travel pathways and choices. Vines and bamboo were used in indoor areas and discarded when dirty. Nesting species were provided with nest boxes. Izard comments that wooden furnishings appear to stimulate species-typical scent marking. Substrate diversity and environmental complexity may also affect the locomotor proficiency of captive golden lion tamarins (Castro *et. al.* 1998, Stafford *et. al.* 1994). Animals living in homogeneous enclosures with large, inflexible, continuous supports exhibited different patterns of locomotion than those in more naturalistic and complex environments with smaller, interrupted, flexible supports.

The kinds of structural items preferred by primates are not easily predicted. Squirrel monkeys preferred rigid perches over non-fixed structures like ropes or swings (Williams *et. al.* 1988). Kopecky and Reinhardt (1991) observed a similar preference in rhesus. Tamarins preferred to use flat surfaces for grooming (Altman *et. al.* 1996). They expressed different forms of play on flat surfaces than on small rounded surfaces (Caine and Boyle 1992). Common marmosets preferred nest boxes with openings facing the room entrance (Kerl and Rothe 1996). Primates of different sexes and ages may prefer different types of structures (Kessel and Brent 1996). Novelty also appears to affect structure use, suggesting some structural items need to be rotated to maintain their enrichment value (Taylor *et. al.* 1997).

Substrates used to cover the enclosure floor can be soft, as are straw, wood wool, shredded paper, wood chips, blankets, vegetation, and soil. These materials can affect space utilization (McKenzie *et. al.* 1986). They may provide comfort, be part of a foraging enrichment strategy, and constitute manipulable items (Westergaard and Munkenbeck-Fragaszy 1985). Hirata *et. al.* (1998) observed two instances of wild chimpanzees using leaves as cushions for sitting on wet ground. The importance of such material for species-typical nest construction in great apes has already been discussed. Many chimpanzee experts consider the provision of bedding material to chimpanzees essential for their comfort (Jane Goodall Institute 1988). Woodchip bedding in outdoor areas for 16 chimps reduced abnormal behavior and helped keep animals dry, without creating any sanitation or health problems (Brent 1992).

When four different types of litter were compared for their effects on the behavior of capuchin monkeys, wood wool and peat proved to be most beneficial at increasing manual foraging and play and decreasing inactivity. Individuals demonstrated a preference for these litter choices. Wood chips were of intermediate value, and they actually avoided corn cob bedding (Ludes and Anderson 1996). Deep litter is used successfully for primate species in many zoos (Dickie 1994). It can be adapted to pharmaceutical laboratory needs (Burt and Plant 1990). Potential health risks associated with these substrates, such as gastrointestinal disorders from ingestion and contamination by pathogens, can be minimized by exercising care in selecting, storing, and handling the materials (Baer 1998b). Drains can be covered indoors and areas spot cleaned rather than hosed daily. Chamove *et. al.* (1982) found after three weeks of use in indoor primate pens, bacterial growth in wood chip litter was actually inhibited.

8. Designing for Social Adjustments

Primate enclosures must not only be adequate for normal postures and movements of independent individuals, but also must be sufficient for social adjustments. The environment should allow individuals to avoid social threats or other noxious stimuli by maintaining sufficient distance or making use of visual barriers, partitions, privacy areas, and escape routes (Applebee, K. A. and P. E. Marshall *et. al.* 1991, Fouts *et. al.* 1989,

Schapiro *et. al.* 1991). Neveu and Deputte (1996) found that, in a group of mangabeys, a reduction in available perches increased social stress and aggression. Bettinger *et. al.* (1994) determined that female chimps in a captive group displayed a preference for opportunities for privacy. Fouts *et. al.* (1989) found that individual chimps preferred different kinds of spaces and parts of the enclosures but their preferences were related to the activities that could take place in them. Other scientists have recommended that captive chimp housing provide opportunities for privacy and have emphasized the importance of small and connecting spaces in addition to larger main areas (Jane Goodall Institute 1988). Rumbaugh (1988) altered the slope of cage fronts to limit violent displays of male chimps towards humans. Bramblett (1989a) emphasizes the value of visual barriers and hiding places for captive guenons. However, in macaque groups certain kinds of visual separation can be detrimental. Erwin (1979) found that aggression and trauma were worse when a group of pig-tailed macaques had access to two visually separated rooms than when the whole group was confined to a single room. The dominant male, who inhibited aggression, could not see group members when they went into the other room and was therefore unable to control violent outbreaks. This finding confirms how important it is for managers to thoroughly understand their species' social structures and behavior and to carefully assess the effects of new environmental changes.

D. Foraging Opportunities

Foraging is a time-consuming event involving searching for, retrieving or acquiring, and processing food.

1. The Goal of Providing Foraging Opportunities

In the wild, animals spend a significant proportion of their time foraging for food. Wild primates may spend 25% to 90% of their waking hours foraging for and eating food (Clutton-Brock and Harvey 1977). Wild primates also have diverse diets which may include browse, seeds, leaves, flowers, fruits, insects, gum, and animal matter. A review of 46 long-term studies of wild populations showed the percentage of food types in primates' diets (leaves, fruits, insects, etc.) is not consistent from month to month. No correlation was observed between the seasonality of the habitat and the degree of dietary variability. This review indicated dietary variability should be part of a feeding enrichment program (Chapman and Chapman 1990).

To promote psychological well-being, it is not sufficient to merely provide a nutritionally adequate diet. It is important to: (1) increase processing time, (2) stimulate the senses by providing foods other than the typical preformulated pellets, and (3) periodically change the availability of food in time and space.

A primary goal of enrichment programs should be to encourage captive primates to spend more time in foraging, not just in eating. Foraging programs require primates to "work" for food items, spend more time processing foods, and increase their exposure to novel foods. In the wild, "working" for food is one of the most frequently found species-typical and time-consuming behaviors, yet many captive primates are deprived of this stimulation. Foraging differs from treat feeding, where food is handed to a primate. Treat feeding can promote trust and bonding between the primate and caretaker and provide short-term sensory stimulation, but it does not generally occupy a significant amount of the primates' time.

In captivity, the variability of food should be considered as well as its nutritional value. Factors to consider in selecting food items for foraging include their manipulative and processing characteristics (i.e., whether they have shells or husks to be removed), as well as their quantity, color, size, novelty, and ability to stimulate the senses. Foraging enrichment programs can add variety to pelleted diets, encourage animals to express their skills discovering and processing natural foods, and increase the time spent in a species-appropriate activity (Noonan 1998, Schapiro *et. al.* 1996b). Mental stimulation may be provided to animals by requiring them to complete cognitive tasks to obtain their food.

2. Research on Foraging

"Under stimulated animals will readily work for food in the presence of freely accessible food. This indicates the gathering and processing of food are rewarding experiences for them independent of caloric intake" (Reinhardt 1997b:89). Researchers noted a willingness of callitrichids to "work" for their food and an increased range of behaviors displayed. When provided a plastic bowl filled with sawdust and pieces of maltcake, some individually housed marmosets were reported to forage up to six hours (Scott 1991). In a zoo setting, juvenile patas monkeys would leap several feet in the air to pull off fruit stuck on branches, even when fruit was available on the ground (McGivern 1994).

In a study comparing the value of several different enrichment methods, Bryant *et. al.* found cynomolgous monkeys preferred foraging activities the most (Bryant *et. al.* 1988). When the behavioral profiles of wild squirrel monkeys were compared with those of a captive colony, total foraging manipulations were found to be seven times more common in the wild than in the captive subjects. Five different enrichment devices were then provided to this colony of 16 single-housed squirrel monkeys. The devices manipulated the most, increasing captive foraging times, were a capped PVC pipe with dispenser holes and two liter plastic beverage containers (Boinski *et. al.* 1994).

Captive animals do not have the time-consuming foraging tasks their counterparts in the wild have, and, finding their time unoccupied, may self mutilate, over groom, or become aggressive. Chamove *et. al*. (1982) tested the effect of ground-foraging opportunities on aggression levels in primate groups among six different species. When fruit scattered over the bare floor was covered by wood chips, levels of aggression were significantly reduced among all but the most arboreal species.

Another study--of two long-term stable groups of rhesus macaques (*Macaca mulatta*)--showed when wood chips, monkey chow, and sunflower seeds were used, there were no changes in the occurrence of agonistic behavior. The greatest behavior changes were produced by the scattered sunflower seeds, which increased activity and foraging and decreased passivity and social interaction. The authors speculated the lack of an effect on agonistic behavior and play were probably due to the groups' long-term structure, stability, and low frequency of abnormal behaviors exhibited before the study began (Byrne and Suomi 1991).

When eight individually-housed 7 to 10 year old rhesus macaques were given astroturf-covered boards and allowed to forage for either Crumbles (from Bioserve, Inc.) or broken up monkey chow (NIH Open Formula Extruded Non-Human Primate Diet), they exhibited a significant decrease in repetitive locomotion and stereotypic behaviors. Some of the monkeys had groomed to the point of baldness, and the condition of their coats improved during this study. The total amount of time spent in consumption behaviors increased to 52% when particulate food was made available (Bayne *et. al.* 1992b)

Brent and Long (1995) found that supplying singly housed female baboons with a PVC feeding device and simply giving regular chow more often during the day each reduced abnormal behaviors. The authors recommend a balance of "feeding devices and frequent feedings." But Novak *et. al.* (1998) found that puzzle feeders which required foraging manipulation to obtain supplementary treats were significantly more effective at reducing locomotor stereotypies in single-housed rhesus than treats alone. Unfortunately, these benefits lasted only for as long as monkeys manipulated the device, about 1 hour after filling. Increasing the level of difficulty did not help and caused animals to give up. This suggests that foraging opportunities must be sufficiently time-consuming, but not too difficult, to have a sustained effect. It is important to recognize the crucial difference between time-consuming foraging activity and treat provisioning without associated foraging.

Singly housed yearling rhesus monkeys were provided five different feeding enrichments sequentially during the work day. These enhancements included Astroturf foraging mats, polyvinyl chloride (PVC) foraging trees, acrylic food puzzles, frozen juice cups, and fresh produce. As a result, these monkeys spent significantly more time playing and less time self-grooming than control monkeys did. The behavioral changes observed were species-typical (Schapiro and Bloomsmith 1995).

In another study, when macaques were given fleece pads sprinkled with food crumbles, they foraged for up to 27 minutes an hour, and their stereotypic behaviors decreased by 73%. When the crumbles were consumed, the monkeys continued to use the fleece for grooming (Lam *et. al.* 1991). Agonism has been decreased by foraging enrichment methods that distribute food and reduce the possibility of dominant individuals monopolizing it (Lee 1983, Lutz and Novak 1995, Southwick 1967).

Feeding fibrous browse materials reduces regurgitation/reingestion in gorillas (Gould and Bres 1986) and appears to reduce coprophagy in chimpanzees (Fritz *et. al.* 1992).

A decrease in wasted food is another tangible benefit observed when primates are required to work for their daily rations. During *ad libitum* feeding, up to 50% of the acquired food may be wasted. When foraging, primates eat almost all food they acquire. Cost of setting up foraging enrichment devices may be offset by savings from non-wasted food (Rosenblum and Andrews 1995).

Some enrichment strategies, like use of a deep wood chip litter in the outdoor pen for groups of stump-tailed macaques, have surprising benefits. Odors were found to be less objectionable in enclosures filled with wood chips and cleaned every four weeks than in bare floor runs cleaned every other day. Hours spent cleaning were considerably fewer, and the cleanliness of monkeys' hair coats improved (Chamove and Anderson 1979). Improvements in tail alopecia and coat condition were observed among members of a group of laboratory common marmosets when wooden bases were added to the bottoms of their metal nest boxes and the marmosets were allowed access to shavings in the base trays. With these changes, the cages stayed cleaner and drier (Sainsbury 1990).

3. Specialized Foraging Adaptations of Different Species

When foraging techniques are employed, species characteristics must be considered. Are the primates leaf, gum, insect, or fruit eaters? Are they mainly terrestrial or arboreal foragers? How do they forage? What body positions do they take? How do they use their hands? Do they use tools? Do they tooth scrape for gums? Levels of cognitive ability and manual dexterity vary and will determine what foraging techniques offered are effective.

Primates have a variety of specialized foraging adaptations and preferences. In the wild, ring-tailed lemurs prefer fresh new leaves, while brown lemurs prefer mature leaves. Lemurs do little processing of fruit and chew and lick the end of bananas rather than peel them (Jolly 1985:48). Golden lion tamarins forage mostly by manipulation: sifting, searching for holes, pulling off bark, and breaking open wood. In contrast, cotton-top tamarins are opportunistic foragers, looking for insects in dense branch and vine tangles (Steen 1995). Lorises capture slower moving and generally unpalatable prey, while galagos take more rapid and palatable prey (Charles-Dominique 1977:40).

Patas monkeys were observed to use browse more for bark chewing than for leaf eating and preferred poplar trees (*Populus sp.)* Due to their paw-like hands, patas are more adapted to terrestrial than to arboreal habitats and are less likely to use tools or perform tasks that require manual dexterity. For patas to access the bark on their browse, metal sleeves were used to hold the browse off the floor in a more natural position

(McGivern 1994).

Captive squirrel monkeys carefully inspect new surfaces by licking, sniffing, and touching, whereas capuchins explore by persistent manipulation (Fragaszy and Adams-Curtis 1991). Great apes and a few monkey species (capuchins, baboons, and macaques) explore the properties of objects and relate them to one another, a skill that is necessary for tool use. Almost all wild chimpanzees can use tools as a part of foraging, notably for termite or ant fishing and for nut cracking. Although the other apes and the monkey species listed above rarely use tools in the wild, they readily use them in captivity. Tools and methods for food acquisition can be provided for these captive primates (Tomasello and Call 1997:57-99).

The type of food and where and how it is obtained in the wild needs to be considered when providing food in captivity. Knowing what foods are relished by the species involved can be useful in selecting special treats. Rhesus macaques were trained to urinate inside or on top of an isolation cage in their outdoor pen by use of preferred food reinforcements such as raisins and grapes (Byrne and Suomi 1991).

4. Forage Placement

One method to enrich a captive environment is by manipulating the availability of food in time and space. Foraging opportunities can be presented in a variety of ways, either naturally or with devices. An outdoor environment allows primates to forage in a natural way if food is placed on the ground or in trees as it would be found in nature. This environment can be imitated by scattering food in a foraging substrate (such as wood chips, shavings, straw, hay, leaf litter, or shredded paper) on the bottom of the enclosure. Food hidden throughout the enclosure allows primates to hunt for it. Hidden food items may include fruits, vegetables, seeds, popcorn, cereals, nuts, and raw pasta. Whole fruit or vegetables to be husked, shelled, or peeled by the primate before eating can also be provided. In one study, cage sterotypies were reduced when corn on the cob was offered to singly housed baboons (Bennett and Spector 1989).

Aggression and monopolization by dominant individuals can be prevented in group housing situations by offering food in multiple locations. One zoo study decreased food competition by scatter feeding food treats. In this study, four different feeding methods were presented to groups of monkeys: Diana monkeys (*Cercopithecus diana*), Allen's swamp monkeys (*Cercopithecus nigroviridis*), lion-tailed macaques (*Macaca silenus*), and Hamlyn's monkeys (*Cercopithecus hamlyni*). The group enclosures had indoor and outdoor areas and straw placed on floors and wire roofs. Cut up apples and oranges were scattered on the roof or floor or presented all in one pile on the roof or floor. Comparisons were made of food consumption and rates of acquisition, foraging, and aggression. The time the monkeys spent to acquire their food was found to be the longest when the food was scattered on the roof. The food scattered on the floor took the monkeys the second longest time. The method of presenting food in single piles resulted in some individuals getting little or no food, so this method is discouraged. There were no significant differences in the aggressive interactions that occurred under the four conditions. This study suggests scatter feeding leads to more equitable food distribution, similar rates of acquisition, and increased foraging times (Buchanan-Smith 1995).

At Chester Zoo in the United Kingdom, arboreal species are fed fruits and vegetables on the mesh roof of their cage to mimic spatial distribution of fruit in nature. Roof feeding encourages an increase in a variety of locomotor postures and muscle use, which in turn promotes physical fitness (Britt 1993). When food is presented this way, the primates climb, perch, balance, and hang to retrieve it. Species like woolly monkeys and spider monkeys can then exhibit suspensory foraging postures.

5. Foraging Devices

Foraging devices range from feeder boxes presenting standard primate chow in novel ways to specially designed boards and puzzles for testing the manipulative and cognitive skills of the species. When standard feeder boxes were remounted onto the square mesh (22 X 22 mm) of the front of cages, individual rhesus macaques took an average of 18.3 minutes to extract the biscuits, compared to 0.2 minutes to collect the biscuits from regular box feeders (Reinhardt 1993a). A foraging device presented to singly-housed cynomologous macaques was preferred over the standard hopper style feeder, and self-directed behaviors were significantly reduced over baseline values. Using it with novel foods and as part of a rotation program renewed interest in the device (Holmes *et. al.* 1995). Distributing group housed macaques' daily standard biscuit ration on top of their chain-link ceiling enclosure increased their foraging time more than 50 fold over putting it in feeder boxes (Reinhardt 1997b).

Astroturf can be attached to boards or hanging logs (Bollen 1995), and small food items such as raisins and seeds stuck into it for the primates to extract. More complex foraging devices have been invented and shown to be useful in occupying primates' time and interest. These include acrylic food puzzles (Schapiro *et. al.* 1991), various shaker boxes and toys, and peg boards placed outside enclosures where food has to be manipulated with "tools" to pull it through the peg maze.

Foraging devices can be made more complex by suspending them from the ceiling. The movement of these hanging devices is especially unpredictable when two primates use them simultaneously (Buchanan-Smith 1997). A challenge was presented to spot-nosed guenons and white-faced capuchins by placing food treats in a free-spinning feeder log hung on a wire out of easy reach (Dorian 1993).

Other novel ways to present food treats include: pine cones stuffed with peanut butter and raisins, juices frozen in cups or ice cube trays, seed and flour paste painted on walls and other objects, fruits and vegetables frozen or speared and hung on bamboo canes. Food may also be scattered in the bottom of pools of water or hidden in cardboard rolls stuffed with shredded paper.

As is the case with other types of enrichment strategies, different species, age groups, and individuals may prefer different types of foraging devices (C. Watson 1997). Not all foraging devices are effective in a given situation (Lutz and Farrow 1996), and facilities may need to try several methods.

6. Foraging for Insects

Live insects also give primates a chance to work for their food. Live prey allows primates to stalk, grab, poke, and pry for their food. Live prey can include beetles, caterpillars, moths, grasshoppers, locusts, ants, crickets, mealworms, butterflies, centipedes, millipedes, spiders, slugs, snails, and frogs. Due to potential health concerns, most captive primates are fed only crickets and mealworms for insect prey. These can be obtained from commercial breeders. Live goldfish in fishing pools have been used as prey for some species such as squirrel monkeys (King and Norwood 1989).

McKenzie *et. al.* discovered captive cotton-top tamarins (*Saguinus oedipus)* made few visits to the cement floor of their enclosure until it was deeply covered with wood chips and scattered with grains and insects. Unlike their wild counterparts, the mostly arboreal primates easily learned to use the ground when given a reason to do so (McKenzie *et. al.* 1986). Although the ground foraging is not a species-typical behavior, the insect feeding is (Rowe 1996:75).

Insects such as crickets or mealworms can be provided in either passive or active dispensers. Passive dispensers such as PVC pipes or milk jugs with small holes in them can be hung from enclosure ceilings or walls to allow slow dispersal of the live prey. Active dispensers require the primate to work to obtain the prey. The PVC or bamboo devices have holes sized so the primate can reach in with a finger, hand, or arm and retrieve prey hidden in the bran, sawdust, or similar materials inside it. Active dispensers can also be used with other food items (Banchero 1995, Demlong 1993, Glick-Bauer 1997, Steen 1995, Wassel and Race 1994).

7. Gum Feeding

Exudate or gum feeding occurs in 45 species of animals, including prosimians, marmosets, tamarins, and Old World monkeys (Kelly 1993). The specialized diets of these primates need to be considered and a similar eating method provided. Gum arabic is an ingredient in many food products, including bakery, confectionery, dairy, and frozen dessert products. Commercial sources of gum arabic (from *Acacia senegal*) are available. The gum mixture can be presented in free-hanging liquid dispensers, holes drilled in branches, logs, or trees, or specially made dowels (Brennan and Russel 1986, LeBlanc 1993). Besides providing enrichment and enhancing visitor viewing, gum-feeders benefit marmosets by increasing their level of activity and visibility for head counts and health observations, and the acceptability of medications mixed with gum and given by syringe (Kelly 1993).

8. Water

Water can be useful as part of an enrichment technique. Wild primates obtain water by mouth, by cupping it in their hands, or by using leaves as sponges. Besides drinking it, they use water in other ways. Japanese macaques were observed submerging potatoes and grains to remove sand and grit (Itani and Nishimura 1973). Several species of macaques dive and swim to obtain food (Malik and Southwick 1988, Suzuki 1965). Standing and running water elicited a broad range of species-typical behavior in group housed rhesus macaques. Females exhibited tool use, and many of the primates soaked their primate chow in the water before eating it. Almost all the macaques also used the water trough as a secondary drinking source. Use of a water trough proved to be a novel, simple, and inexpensive enrichment technique (Parks and Novak 1993).

9. Browse

Fresh browse is a great source of natural enrichment. The National Zoo has a list of approved East Coast browse species they feed to their animals. These include: alder, amaranths, arborvitae, aspen, bamboo, beech, birch, bush honeysuckle, butterfly bush, cattails, chicory, clover, comfrey, cotoneaster, cottonwood, daylily, dogwood, elaeagnus, elm, fig, forsythia, grasses, greenbriers, hackberry, hawthorn, hazelnut, hibiscus, Japanese silver grass, kerria, kudzu, linden, maple (except red maple), mock orange, mulberry, nasturtium, Oregon grape holly, pear, pickerelweed, poplar (except tulip poplar), purslane, raspberry and blackberry, redbud, rose, snowberry, violets, water hyacinth, and willow (Shumaker 1995).

An herb garden was provided to woolly monkeys housed outdoors in a zoo (Vermeer 1994). Herbs were grown in a wood box covered with wire mesh. Roots were protected by allowing the monkeys to access only plant parts growing above the mesh. Species of herbs were chosen which had medicinal compounds effective against the typical health problems of these monkeys. In addition to treating potential illness and stress, the herbs provided variation in taste and diet. Insects were attracted to the flowers of the herbs and provided additional dietary variety. Other monkeys who showed an interest in the herb gardens included sakis, marmosets, tamarins, capuchins, lemurs, and squirrel monkeys.

In a study of six chimpanzee groups at three different sites, 13 plant species were identified as being used for their medicinal value. Chimpanzees chew the pith of plants, swallow whole leaves, and eat other items of possible medicinal value such as bark, wood, termite mound clay, and saponin-rich berries. Often these food items are extremely bitter and even toxic in certain amounts. The value of these plants is believed to be related to control of parasites and gastrointestinal disorders, regulation of fertility, and possible antibacterial or antihepatotoxic activity (Huffman and Wrangham 1994).

10. Other Considerations

Since there may be striking individual preferences for different foods, various foraging items should be tried even if they are not usually given to members of that species. However, some precautions are needed for using food as environmental enrichment. Because extra food over the normal diet could result in obesity, weights may have to be monitored, and amounts fed adjusted. Increasing the level of difficulty too much in a foraging program may cause distress and will not necessarily increase foraging behavior (Novak *et. al.* 1998). All aspects of an enrichment program, including foraging strategies, need to be evaluated on a continual basis to address any potential problems and make necessary adjustments.

E. Manipulanda

Manipulanda are objects that can be moved, used or altered in some manner by the primate's hands. Monkeys and apes readily handle a variety of objects during play, display, grooming, and sexual behavior (Schapiro *et. al.* 1991:22). Primates often choose to manipulate items with their mouths as well as their hands. The items may be artificial or natural. They may be durable or easily broken, taken apart, destroyed, shredded, or used up. "Toys" such as balls, chew toys, etc., immediately come to mind in this category, but other objects associated with food, bedding, or moveable structures also qualify as manipulanda. Also included are mechanical devices such as electronic game machines which primates learn to use. Some of these even permit interaction with caretakers and the public (Markowitz 1981).

Primates have excellent dexterity, which they combine with advanced intelligence to solve problems. Some species, such as capuchins and great apes, are extremely dextrous, others have limitations due to anatomical and behavioral differences (Visalberghi 1990, Westergaard and Munkenbeck-Fragaszy 1985). Tool use, once thought to be unique to humans, has been documented among wild and captive primates (Beck 1980, Chevalier-Skolnikoff 1990, Phillips 1998, Starin 1990,). Sugiyama (1995) describes chimpanzees using different leaf species as spoons or sponges to drink water or sap. Captive mustached guenons (*Cercopithecus cephus)* may use an oat straw as a grooming tool (Maxwell 1993). Toys and other objects to manipulate are excellent forms of enrichments. These items must be chosen wisely to suit the species involved.

Examples of manipulanda are:

- Large, moveable objects such as bowling pins, highway cones, buckets, milk crates, and barrels
- Medium sized semi-durable items such as PVC joints and plastic containers (jugs and bottles)
- Small, rubber and plastic balls, rings, chains, and squeeze toys
- Rawhide and soft rubber chews
- Frozen items (ice cubes, fruit juices, fruits and vegetables) and ice blocks with items in them
- Soft cloth items such as stuffed animals, blankets, sheets, and burlap sacks
- Wooden branches, twigs, browse, dowels, and blocks
- Paper and paper products (bags, butcher paper, newspapers, magazines, and telephone directories)
- Cardboard products such as carpet and towel tubes and boxes stuffed with shredded paper.

When toys are new they stimulate curiosity and may increase play behavior. Animals, however, lose interest in or habituate to toys over time (Cardinal and Kent 1998, Paquette and Prescott 1988, Taylor *et. al.* 1997). Rotating toys on the basis of texture, shape, and color helps to maintain interest (*NRC/IlLAR* 1998:17).

Enrichment techniques can be used to target a variety of species-typical behaviors and activities. Hiding fruit in a cardboard roll stuffed with shredded paper stimulates exploration and increases processing time. The cardboard roll can be manipulated and played with following food retrieval (Banchero 1995). The goal of providing manipulanda is to increase the time that a primate is engaged in manipulatory behaviors similar to those exhibited in the wild.

Manipulable objects have been effective in increasing species-appropriate behavior and decreasing abnormal behavior in many instances (Bayne *et. al.* 1992a, Brent and Belik 1997, A. S. Clarke *et. al.* 1982, Eaton *et. al.* 1993, Kessel and Brent 1998a, Westergaard and Munkenbeck-Fragaszy 1985). In some cases, they have not been effective (Line *et. al.* 1991b, Spring *et. al.* 1997). Not all items are equally interesting to a primate (Brent and Stone 1996, Bryant *et. al.* 1988, Cardinal and Kent 1998).

Wilson's 1992 study of captive great apes showed the importance of customizing objects for the species using them (S. Wilson 1992). Young gorillas often used objects such as browse or toys to interact with other animals. In a typical interaction, they would give another animal a playful swat with a branch and run. Orangutans on the other hand preferred to manipulate burlap sacks, boxes, or hay while remaining in one position. The gorillas appeared more active than the orangutans and chose objects they could easily carry with them. Wilson also concluded the number of animals within the enclosure played a large part in determining how active the animals were.

Having objects to manipulate may be particularly important for primates that are socially restricted (Boinski *et. al.* 1999, Crockett *et. al.* 1989, Eaton *et. al.* 1993). Schapiro and colleagues found singly-housed rhesus macaques used inanimate enrichment more than rhesus living in social groups (Schapiro *et. al.* 1996a, 1997a). However, Novak *et. al.* (1993) found older, socially housed rhesus also used toys quite frequently. [Also see

Line *et.al* (1991b) on this subject.] Toys reduced abnormal behavior in group-housed baboons (Brent and Belik 1997) and single-housed pig-tailed macaques (Kessel and Brent 1998a). However, for chimpanzees, Brent and Stone (1996) found social housing had no effect on object use. Dominance status may also play a role in whether a primate will use an object (Novak *et. al.* 1993).

Most objects are designed to stay inside the enclosure, but some hang on the outside. Some objects are meant to be indestructible, however many primates are motivated to destroy them. Some objects are provided with the intent they be shredded or chewed (Pruetz and Bloomsmith 1992).

As with human children, care must be taken to ensure objects given to primates are reasonably safe for the species: that they cannot injure their hands on them; that they do not chew and swallow harmful amounts of them (if they are inedible); that they do not become inescapably entangled in them (as with a long chain) (Murchison 1993). Some types of manipulanda must be periodically cleaned or removed. The amount of labor involved and the costs vary. The benefits to the animals must be weighed against the costs and potential risks. "Straw and burlap bedding, cargo nets, and destructible (and edible) objects can be injurious to animals, but if they are carefully selected and the animals frequently observed, we believe that the benefits of many of these types of objects outweigh their potential harm" (*NRC/ILAR* 1998:17).

It is important for an animal to feel that it has some control over its environment (Markowitz and Aday 1998). This could be one reason why simple, destructible objects are often preferred by primates over more complex indestructible ones (Bryant *et. al.* 1988, Sambrook and Buchanan-Smith 1997). Kessel and Brent (1998) also suggest providing multiple objects is a way to increase choice and control. Multiple objects in social groups also help ensure dominant animals cannot monopolize the objects.

It is also important the animal has the ability to escape from the object if threatened by it. Sometimes a novel object or situation will evoke "neophobia" or fear in a primate. Careful consideration of species, age, rearing history and other individual characteristics in choosing objects will reduce the likelihood of fear reactions.

The Wisconsin Gnawing Stick is a low cost enrichment item for caged macaques. This branched piece of deciduous tree offers the primate many options. Macaques were observed manipulating, gnawing, nibbling, chewing, hugging, dragging, rolling, playing, and even perching on it. Such activity causes the object to change shape, size, and even texture over time, and thus maintain its novelty and counteract boredom (Reinhardt 1997c).

Manipulanda as a critical element overlaps with two others--structure and substrate in the primates' enclosure and providing foraging opportunities. Manipulable objects play a role in social interactions that must be carefully understood. They also play a small role in permitting infants to develop properly. However, the most important aspect of manipulanda may be that, if selected and used well, they can stimulate several senses and permit the animal to experience novelty and a sense of control over part of its environment.

F. Consideration of Sensory Stimulation

In designing a plan to meet the five critical elements, a facility must also consider stimulation of the five senses, including the visual, auditory, olfactory, tactile and gustatory senses. For example, in choosing housing options under the critical element of Social Grouping, the facility should recognize that permitting primates to live together and communicate with each other provides them with stimulation of most of the senses. Social housing of primates is a rich source of sensory stimulation and should be accomplished whenever possible. If social housing with contact with others of their species is not possible, it is important to provide as much sensory contact as possible, whether it be seeing, hearing, or smelling other primates. The importance of the senses and other methods of providing sensory stimulation are discussed below.

1. Visual

Visual communication is a major source of information between primates. Spacing between individuals, body postures, and facial signals, especially the complex facial signals in hairless-faced monkeys and apes, all convey information. Primate social relations are maintained and changed through the use of visual communication. Visual communications can be analyzed to determine how to manage social relationships (Zeller 1987). Caregivers need to be aware of the importance of visual communication when group housing primates or when arranging single-housing caging.

Large, complex environments with complete social groups offer a rich variety of visual stimulation. Visual stimuli are virtually negligible in small, barren, isolated environments with limited views. Outdoor environments provide natural stimulation from the weather, vegetation, and passing wildlife.

Animals may need temporary visual seclusion as well as stimulation (Bramblett 1989b). The optimum types and levels of stimulation vary between species and individuals. Additional enrichment may be provided by allowing the primate a means of controlling the stimulation (J. Coe 1995).

Many methods of enriching the environment visually involve the use of light, color and motion. Standard stainless steel cages may be altered to provide more light and enable visualization of neighboring primates by replacing bars or metal walls between cages with clear plexiglass panels. It is also helpful to redesign rooms so primates are not kept in darkened, lower-tier cages (Mahoney 1992, Reinhardt 1997c). Giving nocturnal species

such as *Aotus* sp. red or blue lights rather than total darkness during the reverse dark cycle promotes their normal activity levels (Wright *et. al.* 1989). Simulating dawn and dusk by gradually turning on or off the lights is also beneficial.

Color schemes in animal rooms may enrich the environment for both monkeys and human caretakers. Lights of varying colors have been found to affect chimpanzees' behavior. For instance, cool-spectrum light (green) reduced the incidence of anxiety behaviors such as pacing and rocking (Fritz *et. al.* 1997). Sunlight has more ultraviolet radiation than fluorescent light, and there is a peak in the blue-green rather than in the yellow-green region of the visible spectrum. It may produce positive effects similar to those described for the chimpanzees (Thorington 1985). When color dyes were added to dry primate chow and presented to adult and juvenile orangutans, the juveniles consumed more food than previously, and the adults consumed their food in less time. One juvenile showed a definite preference for red chow (Barbiers 1985). Colored objects to manipulate may provide some visual stimulation, especially if they have moveable parts.

Motion can be used as visual stimulation in various forms such as TV, videos, or video games (Brent and Stone 1996, Rumbaugh *et. al.* 1989). Television should only be presented in a way that primates have the choice not to watch it, as some television images may be disturbing.

Several studies have evaluated the ability of audiovisual and computer media to increase the complexity of the environment, especially for singly-caged primates. In one study, the time chimpanzees spent watching videos varied with the content of the tape and with individual preferences (Bloomsmith and Young 1988). Chimpanzees who observed "real" world events on TV seemed to understand the TV monitor (Rumbaugh *et. al.* 1989). Chimpanzees have demonstrated they can learn to use a joystick by watching an experimenter play a game. They have also learned about food locations and events occurring outside their direct view by watching television monitors (Savage-Rumbaugh 1986).

Rhesus macaques have also been found to watch videos and manipulate video game joysticks. They spent more time watching videos than manipulating joysticks. Females showed more interest than males. Both socially and individually housed monkeys became more active (Platt and Novak 1997). Although it did not help as much as puzzle feeders and foraging boxes, short-term viewing of videotapes did decrease some stereotypic behaviors in rhesus with abnormal behaviors (Meunier *et. al.* 1989:479). One study seemed to show videotapes were not as effective as sensory stimulation, but the videotapes used were presented without sound to yearling rhesus housed singly outdoors where they could watch other monkeys and had competing stimuli from the natural environment (Schapiro and Bloomsmith 1995). Rhesus' psychomotor skills and cognitive abilities are often tested with the use of joysticks and computer screen programs. One psychomotor test system consisted of a computer game with a food reward. Monkeys are given free choice to access the game or not. This allowed them to interact with and exert some control over their environment. In experimental protocols related to grading induced Parkinsonian symptoms, test systems such as these are used to determine abnormal psychomotor performance (Rosenberg *et. al.* 1990).

Mirrors have been used in many ways. Some monkeys can perceive a mirror image as their own reflection (Platt and Thompson 1985). They can skillfully direct mirrors toward an otherwise visually unavailable activity or animal (Eglash and Snowdon 1983, O'Neill-Wagner *et. al.* 1997). Small portable mirrors are repeatedly manipulated and remain a source of fascination over a period of months (Anderson 1983).

2. Auditory

Auditory stimuli consist of vocalizations from other primates, sounds from the natural environment, and music. Vocalizations can communicate messages such as danger, fear, and discovery of food, and are important signaling mechanisms between primates (Bayne 1995). Auditory calls are especially important when visual transmission of messages is not possible. Lar gibbons signal territorial ownership by "singing". This singing behavior may also be important to the formation and maintenance of the pair bond (Shepherdson *et. al.* no date). Primate species who practice allomothering have specific play vocalizations which may serve as information sources for maternal retrieval of infants (Masataka and Kohda 1988).

Because vocalizations are an integral part of many species' social structure, they are sometimes used as quantitative indicators of group members' psychological health. A study of three individually housed olive baboons compared animals' vocalizations in enriched and nonenriched environments. When enrichment items were present, there was an increase in the number of certain kinds of grunts believed to be a means to maintain contact. It is possible caretakers can learn to use vocal signals to evaluate animal welfare (Crowell Comuzzie 1993).

Acoustical recordings of primate vocalizations, made continuously or at discrete times, show there are different frequencies and types of vocalizations made in response to various kinds of behavioral and environmental events. Many animals exhibit different vocal patterns depending on their emotional states. Animals also make nonvocal sounds, such as cage-banging, to express their emotions. Rhesus macaques were shown to begin moving vigorously in their cages and emitting anticipatory "coos" in response to the sound of outside footsteps. Wild rhesus give similar "coos" of different intensities to signal excitement or relief. Studying these vocalizations may provide a way to assess the monkeys' emotional states (Mulligan *et. al.* 1994).

Music and naturalistic sounds available at times throughout the day may reduce aberrant behaviors (National Institutes of Health 1991). Socially housed rhesus monkeys given access to a device allowing them to turn music on and off spent a considerable amount of time playing the music. Their interest was maintained longer when they were given a choice between two stimuli, and they showed a preference for jazz and dixieland over animal sounds. Compared to a control group, the rhesus given auditory stimulation showed an increase in affiliative behavior and a decrease in self-

directed behaviors. The study also showed the music had a calming effect during conditions of heightened arousal such as the introduction of a novel or threatening object (Drewson 1989). Although the behavior and blood pressure of a small group of singly caged baboons did not vary when they were given auditory stimulation, their heart rates were significantly lower when the radio was on (Brent and Weaver 1996).

Under certain conditions, auditory stimulation can be aversive and turn into noise. Individually housed monkeys in colony rooms sometimes raise the sound levels quite high. Loud noise has been frequently reported to cause abnormal behavioral and physiological effects (Gamble 1982, Peterson 1980). Sudden unexpected noise can also be disturbing and should be minimized (International Primatological Society 1993). Pregnant rhesus monkeys exposed to unpredictable noise during mid to late gestation had offspring that showed more abnormal social behavior than those in a control group (Clarke and Schneider 1993). High noise levels resulted in sustained blood pressure elevations in rhesus monkeys (Peterson *et. al.* 1984). Primates who could control the volume of loud, continuous white noise showed less stress than animals who could not control it (Hansen *et. al.* 1976). Auditory stimulation seems to be most beneficial when the monkey has some control over it.

3. Tactile

Tactile stimulation is provided by all aspects of a primate's environment, including the materials composing the cage, items placed in the cage such as food and toys , and cage mates. In outdoor enclosures the sense of touch is stimulated by environmental factors such as the sun, rain, and wind.

Group housed primates receive much tactile stimulation when grooming their cage mates. If primates cannot be group-housed so they are together all the time, tactile contact should be allowed with conspecifics or caretakers on a periodic or scheduled basis or through grooming bars (Crockett *et. al.* 1997, Taylor *et. al.* 1998). Macaques who received fleece cushions groomed them using the same motor patterns directed toward monkeys. The fleece pads, with and without forage crumbles, reduced stereotypies by up to 73%. These researchers "strongly recommend provision of separate grooming and foraging substrates" for single housed monkeys (Lam *et. al.* 1991). Tactile stimulation is especially important to infants. Cloth-covered objects are used to provide tactile comfort to surrogate-reared infants.

Physical contact between conspecifics has other psychological benefits. If wild chimpanzees are frightened by an unaccustomed sound, they usually seek physical contact with companions, touching, embracing, or kissing (Goodall 1986). The same calming effect of physical contact is seen with captive chimpanzees (W. A. Mason 1965).

Grooming can be used in operant conditioning as a positive reinforcer. In a study of visual discrimination, when a monkey correctly indicated a pattern, the experimenter groomed the monkey's face, neck, and head with his hand (Taira and Rolls 1996). In research involving 10 coprophagic chimpanzees, treatment consisted of stimulating the tactile senses through the use of various paper media, a combing/brushing schedule, and muscle pressure techniques. The rate of coprophagia was observed to decrease (Struthers 1997).

A floor substrate such as woodchip litter, straw, or leaves provides tactile stimulation to primates when they search through it for hidden food items (Chamove and Anderson 1979, K. C. Baker 1997a, Stegenga 1993). Manipulating artificial turf or fleece as part of a foraging task provides tactile stimulation.

Food has various sense-stimulating properties, including tactile. Whole food manipulation may be an important part of an animal's feeding behavior, but a common practice is to chop food into small portions and distribute it equally among individual animals. In a study in which lion-tailed macaques were given eight different whole or chopped foods, time spent feeding increased when food was presented whole. Unexpected positive results of presenting food whole included: the mean diversity of foods consumed was greater, and total food consumption increased (Lindburg and Smith 1988).

4. Olfactory

Anatomical specializations for olfactory communication are most common among the prosimians, callitrichids, and some Cebidae. Specialized glands in these primates produce volatile, strong-smelling chemicals called pheromones. When individuals scent mark they actively or passively transfer pheromones to objects or locations in their environment to signal their presence. Another type of olfactory signaling is urine washing, where the primate urinates on its tail and feet so these leave a scent trail.

Olfactory communication is used for territorial defense, to foster aggregation of group members, and to signal alarm or aggression (Zeller 1987). In some species, scents indicate not only species and gender, but also individual identities (Epple *et. al.* 1988). One study showed discrimination of predator and non-predator scents is innate in cotton-top tamarins. This underscores the importance of not placing predators and their feces where prey species can smell them (Buchanan-Smith *et. al.* 1993).

Olfactory stimulation is essential for the psychological well-being of scent marking species, and objects must be provided which allow them to mark their environment. Over-cleaning their enclosures needs to be avoided to prevent behavioral problems and skin lesions resulting from an over-stimulated need to scent mark (NRC/ILAR 1998).

Many primates benefit from being provided foods with a variety of different scents. One method of olfactory stimulation is to prepare popcorn in

primates' rooms.

The possibility that colognes, perfumes, and other scented items might have potentially negatively effects should be considered. In one such incident, the first time a zoo keeper wore perfume to work she was bitten by a black and white ruffed lemur (*Varecia vari*). In another zoo, a visitor who used an herbal shampoo had a group of ring-tailed lemurs (*Lemur catta*) jump on her shoulders and begin grooming her hair (W. K. Baker 1997).

5. Gustatory

Although most people consider taste foremost in their food selections, many captive primates are not given much gustatory variety or choice. They are routinely fed diets consisting of commercial monkey biscuits and occasional pieces of fruit. This is an extreme contrast to their natural environment. Fruits compose 60 to 90% of the food intake of wild macaques, and macaques may consume over 100 or more plant species in a year (Lindburg 1991). Wild chimpanzee diets are extremely diverse, consisting of fruit, leaves, stems seeds, other plant parts, animal matter, and inorganic matter (earth, ash, rotten wood). The relative lack of diversity in captive primates' diets restricts their experience of different tastes, textures, consistencies, sizes, and colors of food items. Increasing the variety of a captive diet is the simplest way to increase the variety of sensory characteristics of food (Bloomsmith 1989a).

A project at Duke University Primate Center showed leaves from a number of local plants can be substituted with no adverse effects for the mango leaves sifakas normally eat. The lemurs and sifakas exhibited plant species preferences and seasonal preferences in the plant parts (Pereira *et. al.* 1989b).

Studies have demonstrated that mammalian species have profound differences in their sense of taste. The sweet tasting ability has been the most studied and differs among primate species. Frugivorous species often have high sensitivity to sweetness and may use it as a criterion in food selection (Hellekant and Danilova 1996, Laska 1996, Laska *et. al.* 1996, Pritchard *et. al.* 1994). Species preferences need to be considered in providing gustatory variety.

6. Environments: Natural vs. Artificial, Outdoor vs. Indoor

Few people would argue that natural outdoor environments provide primates with more sensory enrichment opportunities than indoor ones. Outdoor environments provide stimuli caused by weather changes and the sights, smells, and sounds of insects, amphibians, birds, and other animals.

Many primate programs try to create a naturalistic environment indoors with various substrates. The Duke University Primate Center showed for some lemur species even large indoor rooms with naturalistic substrates proved inadequate to promote normal behavior. Reproduction and activity patterns improved when sifakas were provided outdoor space. When given the choice of a large indoor room or a much smaller outdoor extension, the sifakas spent 90% of their time outdoors (Pereira 1991).

One study was conducted to test whether laboratory born and raised rhesus juveniles could benefit from short-term exposure to an outdoor, apparatus-enriched corncrib enclosure next to a semiwooded pasture. During the nine weeks they were outside, they achieved higher scores for locomotion and exploration. They also exhibited less frequent self-oral behavior, a change which remained when they returned to the laboratory environment (O'Neill *et. al.* 1991).

7. Stimulus Poor Environments

Many captive environments contain much less stimulus variety than the natural environment. Environmental enrichment may be of greater importance to primates confined to indoor, stimulus-poor rooms than to those that can go outdoors (Schapiro and Bloomsmith 1995). Sensory deprivation may cause repetitive movement which "can be seen as an animal's attempt to increase its sensory input" (Wemelsfelder 1985: 143). Chamove and Anderson (1989) have suggested that stereoptyped movements, being familiar and repetitive, can also calm an individual when sensory input is too high."

8. Levels of Stimulation--Controlling Exposure

All primates need to be carefully observed to assess how various stimuli affect them. Caretakers can be a major source of stimulation for individually housed primates, but caretakers' mannerisms, voice patterns, and timing of visits may calm or stress these primates (Cooper and Markowitz 1979).

A basic behavioral need for any primate is to have some choice over the stimuli in its environment. Several zoos are now designing group-living enclosures with gradients of environmental choices. Smaller animal enclosures could be equipped with motion detection activation controls to allow primates to exercise choices over conditions such as light intensities, colors, and sound recordings. Options like these compose the next level of enrichment, allowing animals some environmental control (J. Coe 1995).

G. Consideration of Novelty and Control

In designing a plan to meet the five critical elements, a facility must also consider the need to provide the animals with some degree of novelty and control over their environment.

The concept of providing novel objects in promoting psychological well-being of nonhuman primates is an accepted practice (Adams *et. al.* 1992, Bayne *et. al.* 1993a, Bloomsmith *et. al.* 1990, Bryant *et. al.* 1988, Chamove and Anderson 1989, Chmiel and Noonan 1996, Line and Morgan 1991, Line *et. al* .1989a, Preutz and Bloomsmith 1992, Shefferly *et. al.* 1993). Novel objects provide opportunities for animals to interact, use species appropriate behaviors, and expand their captive behavioral repertoire. The use of novel objects has been shown to replace or have therapeutic effects on the abnormal behaviors of caged primates (Bloom and Cook 1989, Line *et. al.* 1989a, Reinhardt 1989).

Novel objects are those which have a relatively high degree of unpredictability to the animal in that many, if not all, of the properties are unknown to it. Objects are usually classified within a range between extremely novel and totally familiar. The more properties of an object that are known to the animal (predictable by it), the less novelty is inherent in the object. Predictability at moderate levels can be beneficial to caged nonhuman primates, but high levels of predictability are considered to be boring. At the other extreme, a high degree of unpredictability may result in extreme stress (Fragaszy and Adams-Curtis 1991, Sambrook and Buchanan-Smith 1997).

When applied generally to enrichment devices and strategies, novelty is variation sufficient to maintain a moderate degree of unpredictability. The variation may be in physical properties such as the size, location, or composition of something, or in the timing or duration that a novel situation is presented. The pelleted food commonly provided to laboratory monkeys is not novel if provided in the accustomed way. However, it may be considered novel if the food is provided in an unusual location and receptacle, such as in a hanging basket the monkeys must swing and reach into, or in small, hidden crevices around the enclosure. If the animal is accustomed to receiving its food in one bin at a certain time of day, one possible novel presentation would be to put parts of it in different locations at different times.

Care must be taken when providing novel objects or situations within an environmental enrichment plan. The type, quantity, and duration of novelty provided must not be distressing to the primates. Usually, the presentation of novel objects to captive primates is considered to be a benign form of environmental challenge (Fragaszy and Adams-Curtis 1991). However, if the animal is restrained, cannot control its distance from the object, or cannot respond appropriately to the object, the presentation may be detrimental to the animal's well-being.

It is important to know the individual animal and its level of anxiety when introducing novelty or environmental change. Anxiety or fearfulness can vary considerably among individual primates (Box 1991). Individual differences in rhesus monkeys and their responses to stress appear to be highly heritable (Suomi 1987). "High-reactive" rhesus monkeys made up 20% of all rhesus monkey groups screened by Suomi and his colleagues (Suomi *et. al.* 1989). The high-reactive monkeys displayed extreme behavioral and psychological responses to environmental novelty. Restrictive mothering styles that do not encourage independence or allow frequent contact with novel objects and situations can diminish the offspring's ability to deal with novelty and change later in life (Altmann 1980, Fairbanks and McGuire 1988, Simpson 1985). There is no single degree of novelty or collection of novel objects and situations that will be appropriate for all captive primates. The National Research Council recommends each facility evaluate its environmental enrichment plans to accommodate individual animal differences (NRC/ILAR 1998).

The use of novelty as enrichment can best be understood by examining two concepts: complexity and controllability (Sambrook and Buchanan-Smith 1997).

1. Complexity

Environmental complexity for nonhuman primates includes the amount and types of interaction with conspecifics, the number and types of structures, substrates, and manipulable objects present, and the amount and types of sensory stimulation provided. The complexity of an object depends upon its visual, tactile, olfactory, auditory, and gustatory properties. An object's or structure's ability to be used in interactions with conspecifics and its ability to stimulate a wide variety of the senses increases its value as an enrichment device.

Novel objects and situations presented to primates do not have to be complex to generate their interest (Bramblett 1989b). However, evidence suggests primates prefer complex stimuli (Humphrey 1972). Traylor-Holzer and Fritz (1985) concluded that primates need a complex environment. Increased cage complexities have also been shown to be beneficial in reducing fighting and inactivity among primates (Chamove and Anderson 1989, Chamove *et. al.* 1982, McKenzie *et. al.* 1986). Tripp (1985) showed an increase in activity associated with corresponding increases in complexity. Increasing complexity also increased the level of manipulation exhibited by capuchins (Westergaard and Munkenbeck-Fragaszy 1985), lion-tailed macaques (Westergaard and Lindquist 1987), and squirrel monkeys (Eterovic and Ferchmin 1985, Fragaszy and Mason 1978, Roy *et. al.* 1978).

Providing complexities in a captive primates' environment stimulates a wide array of natural behaviors. Perches and other climbing structures open up vertical cage space to terrestrial and arboreal species for climbing, hanging, and swinging. Complexities must be geared toward the needs of the primate species involved. For macaques, Kopecky and Reinhardt (1991) showed the benefits of using perches rather than swings and placing the perches at the front of the cage to satisfy their inquisitive nature (Reinhardt 1997a).

Just having several structures and complexities available to a group of primates does not guarantee they will continue using them. A study of

macaques by Taylor *et. al.* (1997) demonstrated novelty performs a significant role in the continued use of play structures. Over time, use of even preferred structures declines. The authors suggest frequent rotation of play structures will provide the animals with opportunities for exploration and maintain their interest. Most novel items, regardless of their complexity, will ultimately become less interesting. Complex environments and objects are novel only as long as some degree of unpredictability is still present. Fragaszy and Adams-Curtis (1991) agree all novel items become familiar over time and explain that there is currently no agreed upon standard for how long an object or condition retains its novelty. The best criterion for determining whether an object or condition is still novel is the animal's interest in it. Facilities must continually evaluate their enrichment programs and rotate objects and conditions or provide new ones as interest in the current ones decreases.

2. Controllability

Controllability is an interactive component of an enriched environment. Sambrook and Buchanan-Smith (1997) consider control to be highly attractive for animals because it is an adaptive aspect of behavior. All primates seek some form of control in their environment. Adjusting to change, altering confronting stimuli, and organizing response strategies, engage their cognitive capacities (Rosenblum 1991).

Caging reduces the degree of control animals have over their environment and outside stimuli (Chamove and Anderson 1989). The ability to exercise some control over stimuli within the caged environment has been shown to reduce stress in captive animals. Rhesus monkeys that had control over noise levels within their environment had lower plasma cortisol levels than monkeys that did not have control (Hanson *et. al.* 1976). Snowdon and Savage (1989) believe animals must feel some sense of control within their environment and be able to generate a positive response from their actions. From the animal's perspective, the exercise of control over changes in the environment is more important than the degree of novelty in the change (Fragaszy and Adams-Curtis 1991). Young rhesus monkeys, given the opportunity to control food and water by manipulating devices, showed less self-directed behavior and more exploration than monkeys who had no control (Mineka *et. al.* 1986). The same study also showed once an animal has been given control, the consequences of removing it may be worse than if the animal had never been given it.

Primates prefer enrichment devices that give them the opportunity to interact with and generate predictable responses from an object. Being comfortable in a captive environment depends on the primate's ability to produce predictable environmental changes through its own actions (Fragaszy and Adams-Curtis 1991). Guenon monkeys prefer responsive objects such as a rattle or maraca that makes a sound when shaken to unresponsive ones like a rattle or maraca with its contents emptied (Sambrook and Buchanan-Smith 1996). Enrichment devices that allow individuals the opportunity to control their environment will be utilized by a larger number of animals and for longer periods of time than nonresponsive objects (Markowitz and Line 1989).

3. Incorporating Novelty and Control into Enhancement Plans

Novelty and control can be incorporated into environment enhancement plans in a variety of ways, including through social interaction, structures and substrates, foraging, feeding and food items, and manipulanda. Each of these topics is discussed below from the point of novelty and control. For more information, the reader should consult the previous sections on these topics.

According to Novak and Suomi (1991) social interaction is widely considered to be the optimal form of enrichment for primates that are naturally social. French and Inglett (1991) state: "The potential for novelty inherent in social interactions is extensive when one considers the myriad of ways in which social partners interact." The housing of two or more familiar individuals together in an enclosure creates many opportunities for novel interactions. Addition of a new social partner presents a complex set of stimuli and provides opportunities to exercise control.

Social housing is the optimal method for providing novelty. However, the presence of social housing should not preclude other types of environmental enrichment. Addition of novel items and complex stimuli into social housing supports the development and expression of complex social behaviors and interactions. The presence of a partner sometimes makes enrichment devices interesting for a longer period of time. Novel electronic games, introduced into several zoos, quickly became familiar and lost their novelty without the give-and-take of a partner (Markowitz and Line 1989, Rumbaugh *et. al.* 1989).

When animals are housed together, access to novel items can sometimes be restricted by factors related to the primates' age and social status. Fragaszy and Adams-Curtis (1991) showed adult male capuchins and infants less than one year of age enjoyed unlimited access to objects introduced into their cage. Access by juveniles one to three years of age was usually dependent on the relative rank of the mother. Placement of novel items within wood shavings, straw, or other substrates can increase the utilization of these items by preventing monopolization by dominant animals. In studies of hamadryas baboons, high ranking individuals were less responsive than lower ranking animals to the introduction of novel objects (Bunnell *et. al.* 1980, Chamove 1983, Menzel 1971). High status monkeys are sometimes more preoccupied with maintaining their social status than with exploring novelty. A thorough knowledge of the social groupings and natural history of each primate species involved is necessary for optimum utilization of novel items.

To incorporate novelty and control into the environment of primates, facilities should take into account the special needs of infants. As previously stated, mothering styles have an effect on an infant's ability to deal with novelty and change (Altmann 1980, Fairbanks and McGuire 1988, Simpson 1985). Young monkeys who are restricted in their social development explore and play less (Suomi 1987). Play and other beneficial social experiences have been shown to increase an individual's ability to respond to change or new environments (Bekhoff and Byers 1985, Fagen 1978,

Geist 1978). Play opportunities may be limited by the number of peers and siblings in the group (Cheney 1978).

The use of novelty and control in structures and substrates is easily demonstrated. Psychological well-being is promoted by adding naturalistic conditions and complex structures that provide opportunities to gain control over and interact with the environment (Snowdon 1991). In Alberta, Canada, the Calgary Zoo has successfully promoted more alert, active, and diverse behaviors by adding leaf piles to its spider monkey exhibit (Stegenga, 1993). Substrates such as straw bedding allow monkeys to produce change in their environment each time they dig in it (Fragaszy and Adams-Curtis 1991). Capuchin monkeys have been shown to use pieces of straw as tools to probe nutboards and other novel objects. Fragaszy and Adams-Curtis (1991) consider straw to be the most important means for providing benign environmental challenge.

Novel food items are an easy way to enrich any captive primate environment. Certain foods, such as coconuts in the husk or corn in the husk enrich primates' environments by creating novel situations (Taff and Dolhinow 1989). Duke University Primate Center successfully incorporated novel and seasonal plant species from North Carolina into the diet of sifakas (Pereira *et. al.* 1989b). Most captive primate diets are restricted to only a few tastes, textures, consistencies, sizes, and colors. In the wild, chimpanzees have been observed to consume between 113 and 205 different foods at various sites (Badrian and Malenky 1984, Hladik 1977, Kano and Mulavwa 1984, Wrangham, 1977). Orangutans (Kortlandt 1984), gorillas (Goodall 1977), and capuchins (Kinzey 1997) eat a wide variety of foods. While the wide variety of foods utilized in nature may not be practically provided for captive primates, any increase in variety will increase complexity and interest in the diet. Novel foods can often be incorporated into foraging devices, hidden in substrates, or presented in novel ways to increase the time needed to find and process them. The use of puzzle feeders and other complex foraging devices allow certain species of primates to manipulate and express cognitive behavior.

Primates use tools more frequently and in more varied ways than any other taxa (Beck 1980, Essock-Vitale and Seyfarth 1987). Their cognitive abilities must be considered when providing manipulanda. Cognitive capabilities present opportunities for primates to respond to environmental conditions in novel ways that may result in additional environmental changes (Box 1991).

Nonhuman primates show a greater variety and complexity of social relations and interactions than any other group of animals (Dasser 1985, Wrangham 1983). This greater complexity of primate social life emphasizes the role of cognition in primates (Box 1991). In singly housed conditions, cognitive stimulation with a variety of manipulanda appears to be more important due to the lack of social complexity and stimulation.

While a certain degree of predictability must be present to provide a comfortable captive environment, total predictability can be boring. Fragaszy and Adams-Curtis (1991) state novelty is present in a system until the individual is certain that all properties within its range of interest are discovered and can be controlled. The challenge of any enrichment program is twofold: (1) to provide novelty that is appropriately stimulating yet non-distressing, and (2) to afford an opportunity for the animal to exert some control over its environment.

Providing social housing, structural complexities, foraging opportunities, and manipulanda that stimulate the senses and incorporate a degree of novelty and control should promote the primates' psychological well-being. However, one should bear in mind that primates have individual personalities and respond differently to novel stimuli. "As with humans, perhaps one monkey's caviar is another's rotten fish." (Novak and Drewsen 1989).

V. REFERENCES AND OTHER SOURCES

A. References

Abee, C. R. (1985). **Medical care and management of the squirrel monkey.** In L. A. Rosenblum and C. L. Coe, eds., *Handbook of squirrel monkey research,* 447-488. Plenum Press: New York.

Adams, B. W., Adair, E. R.,Olsen, M. C., and Fritz, M. S. (1992). **Two squirrel monkey toys.** *Laboratory Primate Newsletter* 31(4): 11-12.

Adams, R. J. and Britz, W. E. (1997). **The baboon suite: novel method to increase the size of a baboon cage to meet the requirements for the care and use of laboratory animals.** *Contemporary Topics in Laboratory Animal Science* 36(4): 70.

Adang, O. M. J., Wensing, J. A. B., and Van Hooff, J. A. R. A. M. (1987). **The Arnhem Zoo colony of chimpanzees: Development and management techniques.** *International Zoo Yearbook* 26: 236-248.

Alford, P. L., Bloomsmith, M. A., Keeling, M. E., and Beck, T. F. (1995). **Wounding aggression during the formation and maintenance of captive multimale chimpanzee groups.** *Zoo Biology* 14(4): 347-359.

Alford, P. L., Nash, L. T. , Fritz, J., and Bowen, J. A. (1992). **Effects of management practices on the timing of captive chimpanzees' births.** *Zoo Biology* 11(4): 253-259.

Altman, J. (1980). ***Baboon Mothers and Infants*.** Harvard University Press: Cambridge, Massachusetts.

Altman, J. W., Knox, K. L., and Sade, D. S. (1996). **Emperor tamarins prefer wide flat surfaces for grooming.** Abstract 668, International Journal of Primatology Congress, Madison, Wisconsin.

Anderson, J. R. (1983). **Responses to mirror image stimulation and assessment of self-recognition in mirror- and peer-raised stumptail macaques.** *Quarterly Journal of Experimental Psychology* 35B: 201-212.

Anderson, J. R., Combette, C. and Roader, J. J. (1991). **Integration of a tame adult female capuchin monkey into a captive group.** *Primate Report* 31: 87-94.

Animal Welfare Act (AWA) §2143(a)(1) 7 U.S.C.

Applebee, K. A., Marshall, P. E.,and McNab, A. M. (1991). **A prototype rhesus cage to satisfy the needs of the Home Office, research, the animal technician, and most importantly, the monkey.** *Animal Technology* 42(1): 23-37.

Asvestas, C. (1998). **Pairing Macaca fascicularis.** *Laboratory Primate Newsletter* 37(3): 50.

Aureli, F. and DeWaal, F. B. M. (1997). **Inhibition of social behavior in chimpanzees under high density conditions.** *American Journal of Primatology* 41(3): 213-228.

Badrian, N. and Malenky, R. K. (1984). **Feeding ecology of *Pan paniscus* in the Lomako forest, Zaire.** In R. L. Susman, ed., *The pygmy chimpanzee: Evolutionary biology and behavior,* pp.275-299. Plenum Press: New York.

Baer, J. F. (1994). **Chapter 5: Husbandry and medical management of the owl monkey.** In Baer, J. F., Wiler, R. E., Kakoma, I., eds., *Aotus: the Owl Monkey.* Academic Press: San Diego.

Baer, J. F. (1998a). Personal communication.

Baer, J. F. (1998b). **A veterinary perspective of potential risk factors in environmental enrichment.** In Shepherdson, D. J., Mellen, J. D., and Hutchins, M., eds., *Second Nature: Environmental Enrichment for Captive Animals,* pp.277-301. Smithsonian Institution Press: Washington, DC.

Baker, K. C. (1996). **Chimpanzees in single cages and small social groups: Effects of housing on behavior.** *Contemporary Topics in Laboratory Animal Science* 35(3):71-74.

Baker, K. C. (1997b). **Human interaction as enrichment for captive chimpanzees: A preliminary report.** *American Journal of Primatology* 42(2): 92.

Baker, K. C. (1997a). **Straw and forage material ameliorate abnormal behaviors in adult chimpanzees.** *Zoo Biology* 16(3): 225-236.

Baker, W. K. (1997). **Question and answer forum.** *Animal Keepers' Forum* 24(10): 434-435.

Baldwin, J. D. (1985). **The behavior of squirrel monkeys (*Saimiri)* in natural environments.** In *Handbook of squirrel monkey research,* L. A. Rosenblum and C. L. Coe, eds. Plenum Press: New York, pp. 35-53.

Banchero, L. (1995). **Leafy activity at the Audubon Zoo.** *The Shape of Enrichment*, 4(2): 8-9.

Barbiers, R. B. (1985). **Orangutans' color preference for food items.** *Zoo Biology* 4(3): 287-290.

Bareham, J. R. (1972). **Effects of cages and semi-intensive deep litter pens on the behaviour, adrenal response and production in two strains of laying hens.** *British Veterinary Journal* 128(3): 153-163.

Bayne, K. A. L. (1989). **Resolving issues of psychological well-being and management of laboratory nonhuman primates.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates*. E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 27-39.

Bayne, K. A. L. (1991). **Alternatives to continuous social housing.** *Laboratory Animal Science* 41(4): 355-359.

Bayne, K. A. L. (1995). **Wildlife management in the laboratory: non-human primates.** In *Wildlife mammals as research models: In the laboratory and field. Proceedings of a seminar sponsored by Scientists Center for Animal Welfare at American Veterinary Medical*

Association meeting, July 12, 1994. K. Bayne and M. Kreger, eds., pp.3-11.

Bayne, K. A. L., S. L. Dexter, J. K. Hurst, G. M. Strange, and E. E. Hill (1993a). **Kong toys for laboratory primates: are they really an enrichment or just fomites?** *Laboratory Animal Science* 43(1): 78-85.

Bayne, K. A. L., S. L. Dexter, and H. Mainzer (1992b). **The use of artificial turf as a foraging substrate for individually housed rhesus monkeys (*Macaca mulatta*).** *Animal Welfare* 1(1): 39-53.

Bayne, K. A. L., S. L. Dexter, and G. M. Strange (1993b). **Effects of food treats and human interaction.** *Contemporary Topics in Laboratory Animal Science* 32(2): 6-9.

Bayne, K. A. L., J. K. Hurst, and S. L. Dexter (1992a). **Evaluation of the preference to and behavioral effects of an enriched environment on male rhesus monkeys.** *Laboratory Animal Science* 42(1): 38-45.

Bayne, K. A. L., H. Mainzer, S. Dexter, G. Campbell, F. Yamada, S. Suomi (1991). **The reduction of abnormal behaviors in individually housed rhesus monkeys (*Macaca mulatta*) with a foraging grooming board.** *American Journal of Primatology* 23:23-25.

Bayne K. A. L. and C. McCully (1989). **The effect of cage size on the behavior of individually housed rhesus monkeys.** *Lab Animal* 18(7): 38-45.

Bayne, K. A. L. and M. Novak (1998). **Chapter 13: Behavioral Disorders.** In *Nonhuman Primates in Biomedical Research: Diseases,* Bennett, B. J., C. R. Abee, and R. Hendrickson, eds., Academic Press: San Diego, pp. 485-500.

Bearder, S. K. (1987). **Lorises, bushbabies, and tarsiers: Diverse societies in solitary foragers.** In *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 11-24.

Beck, B. B. (1980). ***Animal Tool Use.*** Garland: New York.

Bekoff, M. (1994). **Cognitive ethology and the treatment of non-human animal: how matters of mind inform matters of welfare.** *Animal Welfare* 3(2): 75-96.

Bekoff, M. and Byer, J. A. (1985). **The development of behavior from evolutionary and ecological perspectives in birds and mammals.** In *Evolutionary Biology*, M. K. Hecht, B. Wallace, G. T. Prance, eds., Plenum Press: New York, pp.215-286.

Bennett, B. T. and M. R. Spector (1989). **The use of naturally occurring manipulanda to improve the psychological well-being of singly housed baboons.** *Journal of the American Veterinary Medical Association* 194: 1782.

Bennett, C. L. and Davis, R. T. (1989). **Long term animal studies.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp.213-234.

Bernstein, I. S. (1962). **Response to nesting materials of wild born and captive born chimpanzees.** *Animal Behavior* 10 (1-2): 1-6.

Bernstein, I. S. (1991). **Social housing of monkeys and apes: group formations.** *Laboratory Animal Science* 41(4): 329-333.

Bettinger, T., J. Wallis, and T. Carter (1994). **Spatial selection in captive adult female chimpanzees.** *Zoo Biology* 13(2): 167-176.

Blackmore, W. M. (1989). **Solution to psychological enhancement of the environment for the nonhuman primate.** In *Housing, Care and Psychological Well Being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 235-254.

Bloom, K. R. and M. Cook (1989). **Environmental enrichment: Behavioral responses of rhesus to puzzle feeders.** *Lab Animal* 18(5): 25-31.

Bloomsmith, M. A. (1989a). **Feeding enrichment for captive great apes.** In *Housing, Care, and Psychological Well Being of Captive and Laboratory Primates*. E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 336-356.

Bloomsmith, M. A., L. Y. Brent, and S. J. Schapiro (1991). **Guidelines for Developing and Managing an Environmental Enrichment Program for Nonhuman Primates.** *Laboratory Animal Science* 41(4): 372-377.

Bloomsmith, M. A., T. W. Finlay, J. J. Merhalski, and T. L. Maple (1990). **Rigid plastic balls as enrichment devices for captive chimpanzees.** *Laboratory Animal Science* 40(3): 319-322.

Bloomsmith, M. A., S. P. Lambeth, A. M. Stone, and G. E. Laule (1997). **Comparing two types of human interaction as enrichment for chimpanzees.** *American Journal of Primatology* 42(2): 96.

Bloomsmith, M. A., G. E. Laule, P. L. Alford, and R. H. Thurston (1994). **Using training to moderate chimpanzee aggression during feeding.** *Zoo Biology* 13(6): 557-566.

Bloomstrand, M. A. and S. P. Young (1988). **The use of videotapes as enrichment for singly housed chimpanzees.** *American Journal of Primatology* 14(4): 411.

Boccia, M. L. (1989). **Long term effects of a natural foraging task.** *Laboratory Primate Newsletter* 28(2): 18-19.

Boinski S., C. Noon, S. Stans, R. Samudio, P. Sammarco, and A. Hayes (1994). **The behavioral profile and environmental enrichment of a squirrel monkey colony.** *Laboratory Primate Newsletter* 33(4): 1-4.

Boinski, S., S. P. Swing, T. S. Gross, J. K. Davis (1999). **Environmental enrichment of brown capuchins (*Cebus apella*): Behavioral and plasma and fecal cortisol measures of effectiveness.** *American Journal of Primatology* 48(1):49-68.

Boisvert, D. (1997). Personal communication.

Bollen, Kelley (1995). **Primate enrichment.** *Animal Keepers' Forum* 22(5): 162.

Boot, K., A. B. Leussink, and R. F. Vlug (1985). **Influence of housing condition on pregnancy outcomes in cynomolgous monkeys (*Macaca fascicularis*).** *Laboratory Animal Science* 19(1): 42-47.

Bowden, R. (1988). **Primate research and psychological well-being.** *Science* 240:12.

Bowditch, A. P., H. S. Crofts, N. G. Muggleton, P. C. Pearce, S. Prowse, and E. A. M. Scott (1997). **Housing and behavioral testing conditions for long term studies.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome, 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Box, H. O. (1991). ***Primate Responses to Environmental Change.*** Chapman and Hall: New York, 442 pp.

Bramblett, C. (1989a). **Enrichment options for guenons in the laboratory.** *American Journal of Primatology* Supplement 1: 59-63.

Bramblett, C. (1989b). **Mental well-being in anthropoids.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates.* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp 1-11.

Brennan, W. C. and J. Russel (1986). **An artificial gum tree for marmosets.** *Zoo Biology* 5: 45-50.

Brent, L. (1992). **Wood chip bedding as enrichment for captive chimpanzees in an outdoor enclosure.** *Animal Welfare* 1(3): 161-170.

Brent, L. and M. Belik (1997). **The responses of group-housed baboons to three enrichment toys.** *Laboratory Animals* 31: 81-85.

Brent, L. and A. Hughes (1997). **The occurrence of abnormal behavior in group housed baboons.** *American Journal of Primatology* 42(2): 96-97.

Brent, L., A. L. Kessel, and H. Barrera (1997). **Evaluation of introduction procedures in captive chimpanzees.** *Zoo Biology* 16:335-342.

Brent, L., D. R. Lee, and J. W. Eichberg (1989). **Effects of single caging on chimpanzee behavior.** *Laboratory Animal Science* 39(4): 345-346.

Brent, L., D. R. Lee, and J. W. Eichberg (1991). **Evaluation of a chimpanzee enrichment enclosure.** *Journal of Medical Primatology* 20: 29-34.

Brent, L. and K. E. Long (1995). **The behavioral response of individually caged baboons to feeding enrichment and the standard diet: A preliminary report.** *Contemporary Topics in Laboratory Animal Science* 34(2): 65-69.

Brent, L. and A. M. Stone (1996). **Long term use of televisions, balls, and mirrors in enrichment for paired and singly caged chimpanzees.** *American Journal of Primatology* 39(2): 139-145.

Brent, L. and D. Weaver (1996). **The physiological and behavioral effects of radio music on singly housed baboons.** *Journal of Medical Primatology* 25(5): 370-374.

Brinkman, C. (1996). **Caging for adult male macaques *(M. fascicularis*) used in long-term biomedical research.** *Abstract for 2nd World Congress on Alternatives and Animal Use in the Life Sciences, Oct. 20-24, 1996, in Utrecht, Netherlands, Alternatives to Laboratory Animals*, Vol. 24, Special Issue, Oct. 1996, p. 216.

Britt, A. (1993). **Cage top feeding for primates.** *Shape of Enrichment* 2(3): 11.

Broom, D. M. and K. G. Johnson (1993). ***Stress and animal welfare.*** Chapman and Hall: London, England.

Brown, C., R. Goburdhun, A. Kirkwood, and D. Robb (1997). **The housing of non-human primates in the commercial research laboratory.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.-27.09.1996.* [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Bryant, C. E., N. M. J. Rupniak, and S. D. Iversen (1988). **Effects of different environmental enrichment devices on cage stereotypies and autoaggression in captive cynomolgous monkeys.** *Journal of Medical Primatology* 17: 257-269.

Buchanan-Smith, H. M. (1995). **The effect of food distribution on captive old world primates.** *The Shape of Enrichment* 4(1): 12-13.

Buchanan-Smith, H. M. (1997). **Considerations for the housing and handling of New World primates in the laboratory.** In *Comfortable Quarters for Laboratory Animals, Eighth Edition, 1997*, V. Reinhardt, ed., Animal Welfare Institute: Washington, D.C., pp. 75-84.

Buchanan-Smith, H. M., D. A. Anderson, and C. W. Ryan (1993). **Responses of cotton-top tamarins (*Saguinus oedipus*) to faecal scents of predators and non-predators.** *Animal Welfare* 2 (1):17-32.

Buerge, T. and H. Weber (1997). **Primate housing facilities for pharmaceutical research in Switzerland.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren. htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Bunnell, B. H., W. T. Gore, and M. N. Perkins (1980). **Performance correlates of social behavior and organization: social rank and complex problem solving in crab-eating macaques (M. Fascicularis).** *Primates* 21: 515-23.

Burt, D.A. and M. Plant (1990). **Observations on a caging system for housing stump-tailed macaques.** *Animal Technology* 41(3): 175-179.

Byrne, G. D. and S. J. Suomi (1991). **Effects of wood chips and buried food on behavior patterns and psychological well-being of captive rhesus monkeys.** *American Journal of Primatology* 23: 141-151.

Byrne, G. D. and S. J. Suomi (1995). **Development of activity patterns, social interactions, and exploratory behavior in infant tufted capuchins, *(Cebus apella).*** *American Journal of Primatology* 35: 255-270.

Byrum, R. and M. St. Claire (1998). **Pairing female *Macaca nemestrina.*** *Laboratory Primate Newsletter* 37(4): 1.

Cain, N. G. and V. J. O'Boyle (1992). **Cage design and configuration of play in red-bellied tamarins, *Saguinus labiatus*.** *Zoo Biology* 11: 215-220.

Cain, N. G., M. P. Potter and E. Mayer (1992). **Sleeping site selection by captive tamarins (*Saguinus labiatus).*** *Ethology* 90(1): 63.

Canadian Council on Animal Care (CCAC) (1993). ***Guide to the Care and Use of Experimental Animals, Volume 1 (2nd Edition).*** E. D. Olfert, B. M. Cross, and A. A. McWilliam, eds., Canadian Council on Animal Care: Ottawa, Canada, 212 p.

Cant, J. (1988). **Positional behavior of long-tailed (*Macaca fascicularis)* macaques in Northern Sumatra (Indonesia).** *American Journal of Physical Anthropology* 76(1): 29-38.

Capitanio, J. P. (1986). **Behavioral pathology.** *Comparative Primate Biology, Vol. 24: Behavior, Conservation, and Ecology* 24: 411-454.

Capitanio, J. P. (1998). **Social experience and immune system measures in laboratory housed macaques: implications for management and research.** *ILAR Journal* 39(1): 12-20.

Cardinal, B. R. and S. J. Kent (1998). **Behavioral effects of simple manipulable environmental enrichment on pair-housed juvenile macaques (*Macaca nemestrina*).** *Laboratory Primate Newsletter* 37(1):1-3.

Carlstead, K. (1996). **Effects of captivity on the behavior of wild mammals.** In *Wild Mammals in Captivity: Principles and Techniques,* D. G. Kleiman, M. E. Allen, K. V. Thomson, and S. Lumpkin, eds., University of Chicago Press: Chicago, Illinois, pp.317-333.

Castro, M. I., B. B. Beck, D. G. Kleiman, C. R. Ruiz-Miranda, and A. L. Rosenberger (1998). **Environmental Enrichment in a Reintroduction Program for Golden Lion Tamarins.** In *Second Nature: Environmental Enrichment for Captive Animals*, D. J. Shepherdson, J. D. Mellen, and M. Hutchins, eds., Smithsonian Institution Press: Washington, D.C., pp 113-128.

Chamove, A. S. (1983). **Role of dominance in macaque response to novel objects.** *Motivation and Emotion* 7: 213-28.

Chamove, A. S. and J. R. Anderson (1979). **Wood chip litter in macaque groups.** *Animal Technology* 30: 69-74.

Chamove, A. S. and J. R. Anderson (1989). **Examining environmental enrichment.** In *Housing, Care, and Psychological Well Being of Captive and Laboratory Primates*, E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 183-202.

Chamove, A. S., J. R. Anderson, S. C. Morgan-Jones, and S. P. Jones (1982). **Deep wood chip litter: hygiene, feeding and behavioral enhancement in eight primate species.** *International Journal for the Study of Animal Problems* 3(4): 308-318.

Chamove, A. S., G. R. Hosey, and P. Schaetzel (1988). **Visitors excite primates in zoos.** *Zoo Biology* 7(4): 359-369.

Chance, M. R. A., B. Byrne, and E. Jones (1983). **A tandem cage for handling group-living monkeys.** *Laboratory Animals* 17: 129-132.

Chapman, C. and Chapman, L. J. (1990). **Dietary variability in primate populations.** *Primates* 31(1): 121-128.

Charles-Dominique, P. (1977). ***Ecology and Behaviour of Nocturnal Primates: Prosimians of Equatorial West Africa.*** Columbia University Press: New York, 277 p.

Cheney, D. L. (1978). **The play partners of immature baboons during intergroup encounters.** *Animal Behaviour* 26: 1038-50.

Cheney, D. L., R. M. Seyfarth, B. B. Smuts, and R. W. Wrangham (1987). **The Study of Primate Societies,** In *Primate Societies,* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp.1-8.

Chevalier-Skolnikoff, S. (1990). **Tool use by wild cebus monkeys at Santa Rosa National Park, Costa Rica.** *Primates* 31(3): 375-383.

Chivers, D. J. (1991). **Species differences in tolerance to environmental change.** In *Primate responses to environmental change*, H. O. Box, ed., Chapman and Hall: London, England, pp. 5-37.

Chmiel, D. J. and M. Noonan (1996). **Preference of laboratory rats for potentially enriching stimulus objects.** *Laboratory Animal* 30: 97-101.

Chopra, P. K., S. Seth, and P. K. Seth (1992). **Behavioural profile of free-ranging rhesus monkeys.** *Primate Report* 32: 75-105.

Clarke, A. S. and S. Boinski (1995). **Temperament in nonhuman primates.** *American Journal of Primatology* 37(2): 103-125.

Clarke, A. S., C. J. Juno, and T. L. Maple (1982). **Behavioral effects of a change in the physical environment: A pilot study of captive chimpanzees.** *Zoo Biology* 1(4): 371-380.

Clarke, A. S. and M. L. Schneider (1993). **Prenatal stress has long-term effects on behavioral responses to stress in juvenile rhesus monkeys**. *Developmental Psychobiology* 26(5): 293-304.

Clarke, A. S. and R. W. Wrangham (1994). **Chimpanzee arrival pant-hoots: Do they signify food or status?** *International Journal of Primatology* 15(2): 185--205.

Clutton-Brock, T. H. and P. H. Harvey (1977). **Species differences in feeding and ranging behaviors in primates,** In *Primate Ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes,* T. H. Clutton-Brock, ed., Academic Press: New York, pp. 557-584.

Coe, C. L. (1991). **Is social housing of primates always the optimal choice?** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*. M. A. Novak and A. J. Petto, eds., American Psychological Association: Washington, D.C., pp. 78-92.

Coe, C. L. (1993). **Psychosocial factors and immunity in nonhuman primates: a review.** *Psychosomatic Medicine* 55: 298-308.

Coe, C. L., P. Cassayre, S. Levine and L. T. Rosenburg (1987a). **Effects of age, sex, and psychological disturbance on immunoglobulin levels in the squirrel monkey.** *Developmental Psychobiology* 21: 161-175.

Coe, C. L., L. T. Rosenberg, M. Fisher, and S. Levine (1987b). **Psychological factors capable of preventing the inhibition of antibody responses in separated infant monkeys.** *Child Development* 58: 1420-1430.

Coe, J. (1989). **Naturalizing habitats for captive primates.** *Zoo Biology* Supplement 1: 117-125.

Coe, J. (1995). **Opinion: Giving laboratory animals choices.** *Lab Animal* 24(7): 41-42.

Coelho, A. M., K. D. Carey, and R. E. Shade (1991). **Assessing the effects of social environment on blood pressure and heart rates of baboons.** *American Journal of Primatology* 23: 257-267.

Collazo, V. E. (1989). **Male rhesus monkey's unusual behavior: interspecies adoption.** *Laboratory Primate Newsletter* 28(1): 23.

Cooper, D. L., and H. Markowitz (1979). **Handlers effects on contact comfort behaviors of two trios of juvenile chimpanzees in the zoo.** *Psychological Reports* 44: 1015-1018.

Cooper, M. A., R. K. Thompson, I. S. Bernstein, and F. B. M. DeWaal (1997). **The integration of stranger males into a group of tufted capuchin monkeys *(Cebus apella).*** *American Journal of Primatology* 42:102.

Cords, M. (1987). **Forest guenons and patas monkeys: male-male competition in one-male groups.** In *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 98-111.

Crockett, C. M., R. U. Bellanca, C. L. Bowers and D. M. Bowden (1997). **Grooming--contact bars provide social contact for individually-caged laboratory macaques.** *Contemporary Topics in Laboratory Animal Science* 36(6): 53-60.

Crockett, C. M., J. Bielitzki, A. Carey, A. Velez (1989). **Kong toys as enrichment devices for singly-caged macaques.** *Laboratory Primate Newsletter* 28(2): 21-22.

Crockett, C. M., and D. M. Bowden (1994). **Challenging conventional wisdom for housing monkeys.** *Lab Animal* 23(2): 29-33.

Crockett, C. M., C. L. Bowers, D. M. Bowden, and G. P. Sackett (1994). **Sex differences in compatibility of pair-housed adult long-tailed macaques.** *American Journal of Primatology* 32(2): 73-94.

Crowell Comuzzie, D. K. (1993). **Baboon vocalizations as measures of psychological well-being.** *Laboratory Primate Newsletter* 32(3): 5.

Dahl, J. F. (1989). **An inexpensive climate-controlled enclosure for gibbons utilizing appropriate technology,** In *Housing, Care*

and Psychological Well Being of Captive and Laboratory Primates, E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp.323-335.

Dasser, V. (1985). **Cognitive complexity in primate social relationships.** In *Social Relationships and Cognitive Development,* R. A. Hinde, A. Perret-Clemont, and J. S. Hinde, eds., Oxford University Press: New York, pp. 9-22.

Demlong, M. (1993). **Another passive insect dispenser.** *The Shape of Enrichment* 2(2): 6-7.

DeWaal, F. B. M. (1989). ***Peacemaking Among Primates.*** Harvard University Press: Cambridge, Massachusetts, 294 p.

DeWaal, F. B. M. (1991). **The social nature of primates.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*, M. A. Novak and A. J. Petto, eds., American Psychological Association: Washington, D.C., pp. 69-77.

DeWaal, F. B. M. (1993). **Codevelopment of dominance relations and affiliative bonds in rhesus monkeys.** In *Juvenile primates: life history, development, and behavior,* Pereira, M. E. and L. F. Fairbanks, eds. Oxford University Press: New York. Chapter 18, pp. 259-276.

Dickie, L. (1994). ***Environmental enrichment in captive primates: a survey and review.*** Dissertation, Darwin College, Department of Biological Anthropology and the University of Cambridge, 89 p.

Doran, D. M. (1996). **Comparative positional behavior of the African apes.** In *Great Ape Societies,* W. C. McGrew, L. F. Marchant, and T. Nishida, eds., Cambridge University Press: Cambridge, United Kingdom, pp. 213-224.

Dorian, C. (1993). **Feeder logs, swings, and perches for primates.** *The Shape of Enrichment* 2(2): 3-5.

Doyle, R. E., S. D. Davis, and W. C. Thomas (1996). **A cost-effective split level baboon condo.** *Lab Animal* 25(9): 49-50.

Drea, C. M. (1998). **Social context affects how rhesus monkeys explore their environment.** *American Journal of Primatology* 44(3): 203-214.

Drewson, K. H. (1989). **The importance of auditory variation in the home cage environment of socially housed rhesus monkeys (*Macaca mulatta*).** *Dissertation Abstracts International* 50(12-B): 5924.

Dukelow, W. R. and T. Asakawa (1987). **Chapter 39: The squirrel monkey.** In *UFAW handbook on the care and management of laboratory animals, 6th edition,* T. S. Poole, ed., Longman Scientific and Technical: Essex, England, pp. 586-578.

Dunbar, D. (1989). **Locomotor behavior of rhesus macaques on Cayo Santiago.** *Puerto Rican Health Sciences Journal* 8(1): 79-85.

Duncan, I. J. H. (1977). **Behavioral wisdom lost?** *Applied Animal Ethology* 3: 193-194.

Duncan, I. J. H., J. Rushen, and A. B. Lawrence (1993). **Conclusions and implications for animal welfare.** In *Stereotypic Animal Behavior: Fundamentals and Applications to Animal Welfare*, A. B. Lawrence and J. Rushen, eds., CAB International: London, United Kingdom, pp. 193-206.

Eaton, G. G., S. T. Kelley, M. K. Axthelm, S. A. Iliff-Sizemore, and S. M. Shiigi (1994). **Psychological well being in paired adult female rhesus.** *American Journal of Primatology* 33: 89-99**.**

Eaton, G. G., S. T. Kelley, S. A. Iliff-Sizemore (1993). **Rawhide "chew bones" reduce abnormal behavior in individually housed adult rhesus macaques.** *American Journal of Primatology* 30: 308.

Eglash, A. R. and C. T. Snowdon (1983). **Mirror-image responses in pygmy marmosets (*Cebuella pygmaea).*** *American Journal of Primatology* 5: 211-219.

Eichberg, J. W., D. R. Lee, T.M. Butler, J. Kelley, and L. Brent (1991). **Construction of playgrounds for chimpanzees in biomedical research.** *Journal of Medical Primatology* 20: 12-16.

Epple, G., I. Kuderling, and A. Belcher (1988). **Some communicatory functions of scent marking in the cotton top tamarin (*Saguinus oedipus oedipus*).** *Chemical Ecology* 14(2): 503-515.

Erwin, J. (1979). **Aggression in captive macaques: Introduction of social and spatial factors.** In *Captivity and behavior: primates in breeding colonies, laboratories and zoos,* J. Erwin, T. Maple, and G. Mitchell, eds., Van Nostrand Reinhold: New York, pp. 139-171.

Erwin, J. (1991). **Chapter 18: Applied primate ecology: Evaluation of environmental changes intended to promote PWB.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*. M. A. Novak and A. J. Petto, eds., American Psychological Association: Washington, D.C., pp.

Essock-Vitale, S. and R. M. Seyfarth (1987). **Intelligence and social cognition.** In *Primate Societies,* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 452-461.

Estes, R. D. (1991). ***The Behavior Guide to African Mammals Including Hoofed Mammals, Carnivores, Primates.*** University of California Press: Berkeley, California, 611 p.

Eterovic, V. A. and P. A. Ferchmin (1985). **Interaction with objects by group-living *Saimiri sciureus.*** *Puerto Rico Health Science Journal* 4: 121-125.

European Economic Community (EEC) (1986). **Guidelines for accommodation and care of animals.** *Official Journal of European Communities* Vol. 29, 18 December 1986, Annex II, Article 5.

European Primate Resources Network (EUPREN) (1997). *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)].

Fagen, R. (1978). **Phenotypic plasticity and social environment.** *Evolutionary Ecology* 1: 263-271.

Fagen, R. (1993). **Primate juveniles and primate play.** In *Juvenile primates: life history, development, and behavior,* Pereira, M. E. and L. F. Fairbanks, eds. Oxford University Press: New York. Chapter 13, pp. 182-196.

Fairbanks, L. A. (1993). **Juvenile vervet monkeys: establishing relationships and practicing skills for the future.** In *Juvenile primates: life history, development, and behavior,* Pereira, M. E. and L. F. Fairbanks, eds. Oxford University Press: New York. Chapter 15, pp. 211-227.

Fairbanks, L. A. and M. T. McGuire (1988). **Long term effects of early mothering behavior on the responsiveness to the environment in vervet monkeys.** *Developmental Psychobiology* 21(7): 711-24.

Faucheux, B., M. Bertrand, and F. Bourliere (1978). **Some effects of living conditions upon the pattern of growth in the stumptail macaque (*Macaca arctoides*).** *Folia Primatologica* 30: 220-236.

Field, K. J., J. Denny, and G. Kabuki (1992). **Nonhuman primate socialization and environmental enrichment using a transfer tunnel.** *Laboratory Primate Newsletter* 31(2): 5-8.

Fleagle, J. (1998). ***Primate adaptations and evolution.*** Academic Press: San Diego, California, 486 p.

Fleagle, J. G., R. A. Mittermeier, and A. L. Skopec (1981). **Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Surinam.** *Primates* 22(3):361--367.

Fligiel, J. and V. Reinhardt (1994). **Assessing group housing for an aged female rhesus macaque.** *Laboratory Primate Newsletter* 33(4): 10-12.

Fouts, R. S., M. L. Abshire, M. Bodamer, and D. H. Fouts (1989). **Signs of enrichment: toward the psychological well-being of chimpanzees.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates*, E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 376-388.

Fragaszy, D. M. (1985). **Cognition in squirrel monkeys: A contemporary perspective.** In *Handbook of squirrel monkey research.* L. A. Rosenblum and C. L. Coe, eds., Plenum Press: New York, pp. 55-98.

Fragaszy, D. M. (1991). **The expression of natural behavioural repertoires in captivity.** *Primatology Today: Proceedings of the XIIIth Congress of the International Primatological Society*, Elsevier Science Publishers BV: Amsterdam, pp.726-727.

Fragaszy, D. M. and L. Adams-Curtis (1991). **Environmental challenges in groups of capuchins.** In *Primate Responses to Environmental Change*, H. O. Box, ed., Chapman and Hall: New York, pp.237-264.

Fragaszy, D. M., J. Baer, and L. Adams-Curtis (1994). **Introduction and integration of strangers into captive groups of tufted capuchins.** *International Journal of Primatology* 15(3): 399-420.

Fragaszy, D. M. and W. A. Mason (1978). **Response to novelty in *Saimiri* and *Callicebus:* Influence of social context.** *Primates* 19: 311-331.

French, J. A. and Inglett, B. J. (1991). **Responses to novel social stimuli in callitrichid monkeys.** In H. O. Box, ed., *Primate Responses to Environmental Change*. Chapman and Hall: New York, pp.275-294.

Fritz, J. (1986). **Resocialization of asocial chimpanzees.** In *Primates: The road to self-sustaining populations,* K. Benirschke, ed., Springer-Verlag: New York, pp. 351-359.

Fritz, J. (1989). **Resocialization of captive chimpanzees: an amelioration procedure.** *American Journal of Primatology* Supplement 1: 59-86.

Fritz, J. (1994). **Introducing unfamiliar chimpanzees to a group or partner.** *Laboratory Primate Newsletter* 33(1): 5-7.

Fritz, J., S. M. Howell and M. L. Schwandt (1997). **Colored light as environmental enrichment for captive chimpanzees (*Pan troglodytes*).** *Laboratory Primate Newsletter* 36:(2): 1-4.

Fritz, J., S. Maki, L. Nash, T. Martin, and M. Matevia (1992). **The relationship between forage material and levels of coprophagy in captive chimpanzees *(Pan troglodytes).*** *Zoo Biology* 11:313-16.

Fruth, B. and G. Hohmann (1994). **Comparative Analyses of Nest-Building Behavior in Bonobos and Chimpanzees.** In *Chimpanzee Cultures*, R. W. Wrangham, W. C. McGrew, F. B. M. deWaal, and P. G. Heltne, eds., Harvard University Press and The Chicago Academy of Sciences, Cambridge, Massachusetts, pp. 109-128.

Fruth, B. and G. Hohmann (1996). **Nest building behavior in the great apes: the great leap forward.** In *Great Ape Societies*, W. C. McGrew, L. F. Marchant, and T. Nishida, eds., Cambridge University Press: Cambridge, United Kingdom, pp.225-240.

Gamble, M. R. (1982). **Sound and its significance for laboratory animals.** *Biological Reviews* 57: 395-421.

Gebo, D. (1992). **Locomotor and postural behavior in *Allouatta palliata* and *Cebus capucinus.*** *American Journal of Primatology* 26(4): 277-290.

Geist, V. (1978). ***Life Strategies, Human Evolution, Environmental Design: toward a Biological Theory of Health.*** Springer-Verlag: Berlin.

Gerber, P., C. R. Schnell, and G. Anzenberger (1997). **Sociophysiological aspects of short-term separation in common marmosets (*Callithrix jacchus*).** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Gilbert, S. G. and E. Wrenshall (1989). **Environmental enrichment for monkeys used in behavioral toxicology studies.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates*, E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 244-254.

Glick-Bauer, M. (1997). **Behavioral enrichment for captive cotton-top tamarins (*Saguinus oedipus*) through novel presentation of diet.** *Laboratory Primate Newsletter* 36(1):2-6.

Goff, C., S. Menkhus-Howell, J. Fritz, and B. Nankivell (1994). **Space use and proximity of captive chimpanzee mother/offspring pairs.** *Zoo Biology* 13(1): 61-68.

Goodall, A. G. (1977). **Feeding and ranging behavior of a mountain gorilla group(*Gorilla gorilla beringei)* in the Tshibinda-Kahuzi region(Zaire).** In *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes,* T. H. Clutton-Brock, ed., Academic Press: New York, pp.449-479.

Goodall, J. (1986). ***The chimpanzees of Gombe: Patterns of behavior.*** The Belknap Press of Harvard University: Cambridge, Massachusetts, 673 p.

Goosen, C. (1988). **Influence of age of weaning on the behavior of rhesus monkeys.** *Primate Eye* 34:16-17.

Goosen, C., S. Fransen, and M. D. Gommers (1986). **Social aspects of abnormal locomotion stereotypy.** *Primate Report* 14: 166.

Goosen, C., W. Van der Gulden, H. Rozemond, H. Balner, A. Bertens, R. Boot, J. Brinkert, H. Dienske, G. Janssen, A. Lammers, and P. Timmermans (1984). **Recommendations for the housing of macaque monkeys.** *Laboratory Animals* 18: 99-102.

Gould, E. and M. Bres (1986). **Regurgitation and reingestion in captive gorillas: description and intervention.** *Zoo Biology* 5: 241-250.

Gouzoules, S. and H. Gouzoules (1987). **Kinship.** In *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 299-305.

Govindarajulu, P., W. Hunte, L. A. Vermeer, and J. A. Horrocks (1993). **The ontogeny of social play in a feral troop of vervet monkeys *(Cercopithecus aethiops sabaeus)*.** *International Journal of Primatology* 14(5): 701-717.

Gust, D. A., T. P. Gordon, A. R. Brodie, and H. M. McClure (1994). **Effect of a preferred companion in modulating stress in adult female rhesus monkeys.** *Physiology and Behavior* 55: 681-684.

Gust, D. A., T. P. Gordon, M. E. Wilson, A. R. Brodie, A. Ahmed-Ansari, H. M. McClure, and G. R. Lubach (1996). **Group formation of female pig tailed macaques.** *American Journal of Primatology* 39(4): 263-273.

Hanson, J. P., M. E. Larson, and C. T. Snowdon (1976). **The effects of control over high intensity noise on plasma cortisol levels in rhesus monkeys.***Behavioral Biology* 16: 333-340.

Harcourt, A. H. (1988). **Bachelor groups of gorillas in captivity: The situation in the wild.** *Dodo* 25: 54-61.

Harlow, H. F. and M. K. Harlow (1965). **The affectional systems.** In *Behavior of nonhuman primates Vol. II.*, A. M. Schrier, H. F. Harlow, and F. Stollnitz, eds., Academic Press: New York, pp. 287-334.

Harlow, H. F. and M. K. Harlow (1972). **Effects of various mother-infant relationships on rhesus monkey behaviors.** In *Readings in Child Behavior and Development, 3rd. Edition*, C. Stendler-Lavatelli and F. Stendler, eds. Harcourt, Brace, and Jovanovich: New York, pp.201-209.

Harlow, H. F., M. K. Harlow, and E. W. Hanson (1963). **The maternal affectional system of rhesus monkeys.** In *Maternal Behavior of Mammals*, H. L. Rheingold, ed., John Wiley and Sons: New York, pp.254-281.

Heath, M. (1989). **The training of cynomologous monkeys and how the human/animal relationship improves with environmental and mental enrichment.** *Animal Technology* 40: 11-22.

Hediger, H. (1964). ***Wild animals in captivity.*** Dover Publications Inc.: New York, p 207.

Hediger, H. (1968). ***The psychology and behavior of animals in zoos and circuses.*** Dover Publications Inc.: New York, 166 p.

Hellekant, G., and V. Danilova (1996). **Species differences toward sweeteners.** *Food Chemistry* 56(3): 323-328.

Hennesy, M. B. (1984). **Presence of a companion moderates arousal of monkeys with restricted social experience.** *Physiology and Behavior* 33: 693-698.

Hirata, S., M. Myowa, and T. Matsusawa (1998). **Use of leaves as cushions to sit on wet ground by wild chimpanzees.** *American Journal of Primatology* 44(3): 215-220.

Hladik, C. M. (1977). **Chimpanzees of Gabon and Chimpanzees of Gombe: Some comparative data on diet.** In *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes,* T. H. Clutton-Brock, ed., Academic Press: New York, pp. 481-501.

Holmes, S. N., J. M. Riley, P. Juneau, D. Pyne, and G. L. Hofing (1995). **Short term evaluation of a foraging device for non-human**

primates. *Laboratory Animals* 29(4): 364-369.

Home Office, Animals (Scientific Procedures) Act (1989). **Code of Practice for the Housing and Care of Animals Used in Scientific Procedures.** Presented pursuant to Act Eliz. II 1986 C.14 Section 21 (Animals (Scientific Procedures) Act of 1986, Ordered by the House of Commons to be printed 7 February 1989. Her Majesty's Stationery Office, London. Available on line at http://www.homeoffice.gov.uk/hcasp.htm on 12/21/98.

Howell, S. M., M. Matevia, J. Fritz, L. Nash, and S. Maki (1993). **Pre-feeding agonism and seasonality in captive groups of chimpanzees.** *Animal Welfare* 2(2): 153-163.

Huffman, M.A, and R. W. Wrangham (1994). **Diversity of medicinal plant use by chimpanzees in the wild.** In *Chimpanzee Cultures,* R. W. Wrangham, W. C. McGrew, F.B. M. DeWaal, and P. G. Heltne, eds., Harvard University Press: Cambridge, Massachusetts, pp.129-148.

Humphrey, N. K. (1972). **Interest and pleasure: two determinants of a monkey's visual preferences.** *Perception* 1: 395-416.

International Primatological Society (IPS) (1993). **International guidelines for the acquisition, care, and breeding of nonhuman primates. Codes of practice 1-3** *Primate Report* 35: 3-29.

Itani, J. and A. Nishimura (1973). **The study of infrahuman culture in Japan.** *Symposia of the Fourth International Congress of Primatology, Vol. 1: Precultural Primate Behavior.* Karger: Basel, pp. 26-50.

Izard, M. K. (1991). **Chapter 15: Efforts to promote psychological well-being in prosimian primates at Duke University Primate Research Center.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*. M. A. Novak and A.J. Petto, eds., American Psychological Association: Washington, D.C., pp. 137-148.

Jane Goodall Institute, ed. (1988). **Recommendations to USDA on improving conditions of psychological well-being for captive chimpanzees, from the Workshop on Maintenance of Chimpanzees in Captivity for Biomedical Research, December 1-3, 1987 in Washington, DC.** *Journal of Medical Primatology* 17: 116-121.

Jolly, A. (1985). **Evolution of Primate Behavior, 2nd Edition,** Macmillan: New York, p 526 .

Kano, T. and M. Mulavwa (1984). **Feeding ecology of the pygmy chimpanzee(*Pan paniscus)* of Wamba.** In *The Pygmy Chimpanzee: Evolutionary biology and behavior,* R. L. Susman, ed., Plenum Press: New York, pp. 233-274.

Kaplan, K. and B. L. Lobao (1991). **A unique housing system for rhesus macaques.** *Lab Animal* 20(6): 48-50.

Kaumanns, W. (1997). **General aspects of primate keeping and colony management.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Keeling, M. E., P.L. Alford, and M. A. Bloomsmith (1991). **Decision analysis for developing programs of psychological well-being: a bias-for-action approach.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*. Novak, Melinda A. and Andrew J. Petto, eds., American Psychological Association: Washington, D.C., pp.57-68.

Kelly, K. (1993). **Environmental enrichment for captive wildlife through the simulation of gum-feeding.** *Animal Welfare Information Center Newsletter* 4(3): 1-2,5-9.

Kerl, J. and H. Rothe (1996). **Influence of cage size and cage equipment on physiology and behavior of common marmosets.** *Laboratory Primate Newsletter* 35(3): 10-13.

Kessel, A.L. and L. Brent (1995a). **An activity cage for baboons, Part I.** *Contemporary Topics in Laboratory Animal Science* 34(1): 74-79.

Kessel, A.L. and L. Brent (1996). **Space utilization by captive born baboons before and after provision of structural enrichment.** *Animal Welfare* 5(1): 37-44.

Kessel, A.L. and L. Brent (1997). **Rehabilitating a rheboon *(Macaca mulatta X Papio hamadryas cynocephalus*), from single housing to social housing: a case study.** *American Journal of Primatology* 42(2): 121.

Kessel, A.L. and L. Brent (1998). **Cage toys reduce abnormal behavior in individually housed pigtail macaques.** *Journal of Applied Animal Welfare Science* 1(3): 227-234.

King, J.E. and V.R. Norwood (1989). **Free-environment rooms as alternative housing for squirrel monkeys.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates*, E. F. Segal, ed. Noyes Publications: Park Ridge, New Jersey, pp. 102-114.

Kinzey, W. G., (ed.) (1997). ***New World Primates: Ecology, Evolution, and Behavior.*** Aldine De Gruyter: New York, 436 pp.

Kitchen, A. M. and A. A. Martin (1996). **The effects of cage size and complexity on the behaviour of captive common marmosets, *Callithrix jacchus jacchus*.** *Laboratory Animals* 30: 317-326.

Kopecky, J. and V. Reinhardt (1991). **Comparing the effectiveness of PVC swings versus PVC perches as environmental enrichment objects for caged female rhesus macaques.** *Laboratory Primate Newsletter* 30(2): 5-6.

Kortlandt, A. (1984). **Habitat richness, foraging range and diet in chimpanzees and some other primates.** In *Food acquisition and processing in primates,* D. J.Chivers, B.A.Wood, and A. Bilsborough, eds., Plenum Press: New York, pp.119-159.

Kurth, B. and D. Bryant (1998). **Pairing female *Macaca fascicularis***. *Laboratory Primate Newsletter* 37(4): 3.

Lam, K., N. M. J. Rupniak, and S. D. Iversen (1991). **Use of a grooming and foraging substrate to reduce cage stereotypies in macaques.** *Journal of Medical Primatology* 20: 104-109.

Laska, M. (1996). **Taste preference thresholds for food-associated sugars in the squirrel monkey (*Saimiri sciurius*).** *Primates* 37(1): 91-95.

Laska, M., E. C. Sanchez, J. A. R. Rivera, and E. R. Luna (1996). **Gustatory thresholds for food-associated sugars in the spider monkey (*Ateles geoffroyi*).** *American Journal of Primatology* 39(3): 189-193.

Laudenslager, M. L. and M. L. Boccia (1996). **Some observations on psychosocial stressors, immunity and individual differences in nonhuman primates.** *American Journal of Primatology* 39(4): 205-221.

Laudenslager, M. L., J. P. Capitanio, and M. L. Reite (1985). **Possible effects of early separation experiences on subsequent immune function in adult macaque monkeys.** *American Journal of Psychiatry* 142:862-864.

Laudenslager, M. L., D.E. Held, M. L. Boccia, M. L. Reite, and J. J. Cohen (1990). **Behavioral and immunological consequences of brief mother-infant separation: a species comparison.** *Developmental Psychobiology* 23: 247-64.

Laule, G. E. and T. Desmond (1998). **Chapter 17: Positive reinforcement training as an enrichment strategy.** In *Second nature: environmental enrichment for captive animals*, Shepherdson, D. J., J. D. Mellen, and M. Hutchins, eds., Smithsonian Institution Press: Washington, D.C.

LeBlanc, D. (1993) **Tamarins also feed on exudates.** *The Shape of Enrichment* 2(3): 5.

Lee, P. (1983). **Ecological influences on relationships and social structure.** In *Primate Social Relationships*, R. Hinde, ed., Blackwell: Boston, pp.225-229.

Leu, M., C. M. Crockett, C. L. Bowers, and D.M. Bowden (1993). **Changes in activity levels of singly housed long tailed macaques when given the opportunity to exercise in a larger cage.** *Journal of Comparative Psychology* 109(4): 368.

Lindburg, D. (1991). **Ecological requirements of macaques.** *Laboratory Animal Science* 41(4): 315-322.

Lindburg, D. and A. Smith (1988). **Organoleptic factors in animal feeding.** *Zoonooz* 61(12): 14-15.

Line, S. W. (1987). **Environmental enrichment for laboratory primates.** *Journal of the American Veterinary Medical Association* 190(7): 854-859.

Line, S. W., A. S. Clarke, and H. Markowitz (1989a). **Adult female rhesus macaque responses to novel objects.** *Lab Animal* 18(4): 33-40.

Line, S. W., H. Markowitz, K. N. Morgan, S. Strong (1991a). **Effects of cage size and environmental enrichment on behavioral and physiological responses of rhesus macaques to the stress of daily events.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*. M. A. Novak, Melinda and A.J. Petto, eds., American Psychological Association: Washington, D.C., pp160-179.

Line, S. W. and K. N. Morgan (1991). **The effects of two novel objects on the behavior of singly caged adult rhesus macaques.** *Laboratory Animal Science* 41: 365-369.

Line, S. W., K. N. Morgan, and H. Markowitz (1991b). **Simple toys do not alter the behavior of aged rhesus monkeys.** *Zoo Biology* 10: 473-484.

Line, S. W., K. N. Morgan, H. Markowitz, and S. Strong (1989b). **Heart rate and activity of rhesus monkeys in response to routine events.** *Laboratory Primate Newsletter* 28(2): 9-13.

Ljungberg, T., K. Westlund, and L. Rydn (1997). **Ethological studies of well-being in two species of macaques after transition from single-cages to housing in social groups.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).]

Louwerse, A.L., T. Kos, and J. A. R. A. M. Van Hooff (1997). **Resocialization of rhesus macaques.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Ludes, E. and J. R. Anderson (1996). **Comparison of the behaviour of captive white-faced capuchin monkeys (*Cebus capucinus)* in the presence of four kinds of deep litter.** *Applied Animal Behavior Science* 49:293-303.

Lutz, C. K., and R. A. Farrow (1996). **Foraging device for singly housed longtailed macaques does not reduce stereotypies.** *Contemporary Topics in Laboratory Animal Science* 35(3): 75-78.

Lutz, C. K. and M. A. Novak (1995). **Use of foraging racks and shavings as enrichment tools for groups of rhesus monkeys (*Macaca mulatta*).** *Zoo Biology* 14(5): 463-474.

Lynch, R. (1998). **Successful pair housing of male macaques.** *Laboratory Primate Newsletter* 37(1): 4-6.

Lynch, R. and D. C. Baker (1998). **Enrichment and exercise room for free roaming.** *Laboratory Primate Newsletter* 37(1): 6.

Mack, P. A. (1998). Personal communication.

Maclean, J. M., A. F. Phippard, M. G. Garner, G. G. Ouggin, J. S. Howath, D. J. Tiller (1987). **Group housing of hamadryas baboons: a new cage design based upon field studies of social organization.** *Laboratory Animal Science* 37:89-93.

Mahoney, C. J. (1992). **Opinion: Some thoughts on psychological enrichment.** *Lab Animal* 21(5): 27-37.

Malik, I. (1986). **Time budgets and activity patterns in free ranging rhesus monkeys.** In *Primate Ecology and Conservation, Volume 2*, J.G. Else and P.C. Lee, eds., Cambridge University Press: Cambridge, United Kingdom, pp. 105-144.

Malik, I., Southwick, C. H., (1988). **Feeding behavior and activity patterns of rhesus monkeys (*Macaca mulatta*) at Tughlaquabad, India.** In *Ecology and Behavior of Food-Enhanced Primate Groups*. J.E. Fa and C.H. Southwick, eds., Alan R. Liss: New York, pp. 95-111.

Maple, T. L. (1979). **Great apes in captivity: the good, the bad, and the ugly.** In *Captivity and behavior: primates in breeding colonies, laboratories and zoos.* J. Erwin, T. Maple, and G. Mitchell, eds., Van Nostrand Reinhold: New York, pp. 231-232.

Maple, T. L. and L. A. Perkins (1996). **Enclosure furnishings and structural environmental enrichment.** In *Wild Mammals in Captivity: Principles and Techniques,* D.G. Kleiman, M. E. Allen, K.V. Thomson, and S. Lumpkin, eds., University of Chicago Press: Chicago, Illinois, pp.212-222.

Markham, R. J. (1990). **Breeding orangutans at Perth Zoo: twenty years of appropriate husbandry.** *Zoo Biology* 9: 171-182.

Markowitz, H. and C. Aday (1998). **Power for captive animals.** In *Second Nature: Environmental Enrichment for Captive Animals,* D. J. Shepherdson, J. D. Mellen, and M. Hutchins, eds., Smithsonian Institution Press: Washington, D.C., pp. 47-58.

Markowitz, H. and S. W. Line (1989). **Primate research models and environmental enrichment.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp.203-212.

Markowitz, H., V. J. Stevens, J. D. Mellen, and B. C. Barrow (1981). **Performance of a mandrill (*Mandrillus sphinx)* in competition with zoo visitors and computer on a reaction-time game.** *Acta zoologica et pathologica antverpiensia* 76: 169-180.

Marriner, L. M. and L. C. Drickamer (1994). **Factors influencing stereotyped behavior of primates in a zoo.** *Zoo Biology* 13(3): 267-275.

Marriott, B. M., R. W. Marriott, J. Norris, and D. Lee (1993). **A semi-natural habitat for housing small nonhuman primates.** *Journal of Medical Primatology* 22(6): 348-354.

Masataka, N. and M. Kohda (1988). **Primate play vocalizations and their functional significance.** *Folia Primatologica* 50: 152-156.

Mason, G. J. (1991a). **Stereotypies: a critical review.** *Animal Behaviour* 41: 1015-1037.

Mason, G. J. (1991b) . **Stereotypies and suffering.** *Behavioral Processes* 25: 103-115.

Mason, G. J. and M. Mendl (1993). **Why is there no simple way of measuring animal welfare?** *Animal Welfare* 2(4): 301-319.

Mason, W. A. (1965) **Detriments of social behavior in young chimpanzees.** In *Behavior of Non-Human Primates, Vol 2 ,* A. M. Schrier, H. F. Harlow, and F. Stollnitz, eds., Academic Press: New York, pp. 335-364.

Mason, W. A. (1971). **Motivational factors in psychosocial development.** In *Nebraska Symposium on Motivation*. W.J. Arnold and M.M. Page, eds. University of Nebraska Press: Lincoln, Nebraska, pp. 35-67.

Mason, W. A. (1986). **Early socialization.** In *Primates: The Road to Self-sustaining Populations.* K. Benirschke, ed. Springer-Verlag: New York, pp. 321-329.

Mason, W. A. (1991). **Effects of social interaction on well-being: developmental aspects.** *Laboratory Animal Science* 41: 323-328.

Mason, W. A. and G. Berkson (1975). **Effects of maternal mobility on the development of rocking and other behaviors in rhesus monkeys: A study with artificial mothers.** *Developmental Psychobiology* 8: 197-211.

Mason, W. A. and J. P. Capitanio (1988). **Formation and expression of filial attachment in rhesus monkeys raised with living and inanimate mother substitutes.** *Developmental Psychobiology* 21: 401-430.

Mason, W. A. and M. D. Kenney (1974). **Re-direction of filial attachments in rhesus monkeys: dogs as mother surrogates.** *Science* 183: 1209-1211.

Maxwell, J. (1993). **Stimulating natural behavior: enrichment.** *Australian Primatology* 7(4): 17-18.

McGivern, L. (1994). **Small Primate Enrichment at the Calgary Zoo, Part 3: Patas and Spider Monkeys.** *The Shape of Enrichment* 3(2): 8-9.

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

McKenzie, S. M., A. S. Chamove, and A. T. C. Feistner (1986). **Floor-coverings and hanging screens alter arboreal monkey behavior.** *Zoo Biology* 5(4): 339-348.

Mendl, M. and R. C. Newberry (1997). **Social conditions.** In *Animal Welfare,* M.C. Appleby and B. O. Hughes, eds. CAB International: New York, New York, pp. 171-203.

Mendoza, S. P. (1991). **Sociophysiology of well-being in primates.** *Laboratory Animal Science* 41: 344-349.

Mendoza, S. P. and W. A. Mason (1986). **Contrasting responses to intruders and to voluntary separation by monogamous and polygynous New World monkeys.** *Physiology and Behavior* 38: 795-801.

Mendoza, S. P. and W. A. Mason (1989). **Behavioral and endocrine consequences of heterosexual pair-formation in squirrel monkeys.** *Physiology and Behaviour* 46: 597-603.

Menzel, E. W. (1971). **Group behavior in young chimpanzees: responsiveness to cumulative novel changes in a large outdoor enclosure.** *Journal of Comparative Physiology and Psychology* 74: 46-51.

Meshik, V. A. (1994). **Group formation in adult Japanese macaques.** *International Zoo News* 41(3): 5-9.

Meunier, L. D., J. T. Duktig, and M. S. Landi (1989). **Modifications of stereotypic behavior in rhesus monkeys using videotapes, puzzlefeeders, and foraging boxes.** *Laboratory Animal Science* 39(5): 479.

Miller-Schroeder, P. and J. D. Paterson (1989). **Environmental influences on reproduction and maternal behavior in captive gorillas: Results of a survey.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal,ed., Noyes Publications: Park Ridge, New Jersey, pp.389-414.

Milton, K. (1993). **Diet and social organization of a free ranging spider monkey population: the development of a species-typical behavior in the absence of adults.** In *Juvenile primates: life history, development, and behavior,* Pereira, M. E. and L. F. Fairbanks, eds. Oxford University Press: New York. Chapter 12, pp. 173-181.

Mineka, S., M. Gunnar and M. Champoux (1986). **Control and early socioemotional development: Infant rhesus monkeys reared in controllable versus uncontrollable environments.** *Child Development* 57: 1241-1256.

Mineka, S. and S. J. Suomi (1978). **Social separation in monkeys.** *Psychological Bulletin* 85: 1376-1400.

Mitchell, G. D., E. J. Raymond, G. C. Ruppenthal, and H. F. Harlow (1966). **Long term effects of total social isolation upon behavior of rhesus monkeys.** *Psychological Reports* 18(2): 567-580.

Morland, H. S., M. A. Suleman, and E. B. Tarara (1992). **Changes in male-female interactions after introduction of a new adult male in vervet monkey (*Cercopithecus aethiops)* groups.** *Laboratory Primate Newsletter* 31(2): 1-4.

Mulligan, B. E., S. C. Baker, and M. R. Murphy (1994). **Vocalizations as indicators of emotional state and psychological wellbeing in animals.** *Animal Welfare Information Center Newsletter* 5(3): 3-4.

Murchison, M. A. (1993). **Potential animal hazard with ring toys.** *Laboratory Primate Newsletter* 34(1): 1-2.

Nash, L. T. (1993). **Juveniles of neogregarious primates.** In *Juvenile primates: life history, development, and behavior,* Pereira, M. E. and L. F. Fairbanks, eds. Oxford University Press: New York. Chapter 9, pp. 119-137.

National Institutes of Health, Office of Animal Care and Use. (1991). ***Non-human Primate Management Plan.*** U. S. Department of Health and Human Services, Public Health Service, National Institutes of Health: Bethesda, Maryland, p 49.

National Research Council, Institute of Laboratory Animal Resources (NRC/ILAR) (1968). ***Nonhuman primates: standards and guidelines for the breeding, care, and management of laboratory animals, a report*.** National Academy Press: Washington, D.C., 35 p.

National Research Council, Institute for Laboratory Animal Research (NRC/ILAR) (1996). ***Guide for the Care and Use of Laboratory Animals.*** National Academy Press: Washington, D.C., 125 p.

National Research Council, Institute for Laboratory Animal Research (NRC/ILAR) (1998). ***The Psychological Well-Being of Nonhuman Primates: A Report of the Committee on Well-Being of Nonhuman Primates*.** National Academy Press: Washington, D.C., 168 p.

Neveu, H., and B. L. Deputte (1996). **Influence of availability of perches on the behavioral well-being of captive, group-living mangabeys.** *American Journal of Primatology* 38: 175-185.

Newberry, R. C. (1995). **Environmental enrichment: Increasing the biological relevance of captive environments.** *Applied Animal Behaviour Science* 44: 229-243.

Noonan, A. (1998). **The effects of environmental enrichment on the behavior of Hamadryas baboons, *Papio hamadryas*.** *Australian Primatology* 7(4):5.

Novak, M. A. and K. H. Drewson (1989). **Enriching the lives of captive primates: Issues and problems.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed. Noyes Publications: Park Ridge, New Jersey, pp. 161-182.

Novak, M. A., J. H. Kinsey, M. J. Jorgensen, and T. J. Hazen (1998). **Effects of puzzle feeders on pathological behavior in individually housed rhesus monkeys.** *American Journal of Primatology* 46: 213-227.

Novak, M. A., A. Musante, H. Munroe, P. L. O'Neill, C. Price, S. J. Suomi (1993). **Old socially housed rhesus monkeys manipulate objects.** *Zoo Biology* 12: 285-294.

Novak, M. A. and A. J. Petto (1991b). **Perspective on psychological well-being in captive primates.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*. M. A. Novak and A.J. Petto, eds., American Psychological Association: Washington, D.C., pp. 1-7.

Novak, M. A. and S. J. Suomi (1991). **Social interaction in nonhuman primates: an underlying theme for primate research.** *Laboratory Animal Science* 41: 308-314.

Nowak, R.M. and J. L. Paradiso (1983). ***Walker's Mammals of the World, 4th Edition. Vol. 1.*** Johns Hopkins University Press: Baltimore, Maryland, 568 pp.

Olfert, E. D., B. M. Cross, and A. A. McWilliam, (eds.), (1993). ***Guide to the Care and Use of Experimental Animals, Volume 1 (2nd Edition).*** Canadian Council on Animal Care, Ottawa, Canada, 211 p.

O'Neill, P. (1989). **A room with a view for captive primates: Issues, goals, related research and strategies.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates*. E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 135-160.

O'Neill, P.L., M. A. Novak, and S. J. Suomi (1991). **Normalizing laboratory-reared rhesus macaque (*Macacca mulatta*) behavior with exposure to complex outdoor enclosures.** *Zoo Biology* 10(3): 237-245.

O'Neill, P., Price, C., and Suomi. S. (National Institutes of Child Health and Human Development, Laboratory of Comparative Ethology (1990). **Designing captive primate environments sensitive to age and gender: Related activity profiles for rhesus monkeys (*Macaca mulatta*).** American Association of Zoological Parks and Aquariums (AAZPA) Regional Proceedings 1990. Northeastern Regional Conference, Washington, D.C. 29 April - 1 May, 1990, pp. 546-551. AAZPA, Wheeling, WV.

O'Neill-Wagner, P., A. C. Wright, and J. L. Weed (1997). **Curious responses of three monkey species to mirrors.** *American Zoo and Aquarium Association (AZA) Regional Conference Proceedings* 95-101. AAZPA, Wheeling, WV.

Palombit, R. A. (1992). **A preliminary study of vocal communication in wild long-tailed macaques: II. Potential of calls to regulate intragroup spacing.** *International Journal of Primatology* 13(2): 183-207.

Paquette, D. and J. Prescott (1988). **Use of novel objects to enhance environments of captive chimpanzees.** *Zoo Biology* 7: 15-23

Parks, K. A. and M. A. Novak (1993). **Observations of increased activity and tool use in captive rhesus monkeys exposed to troughs of water.** *American Journal of Primatology* 29(1): 13-25.

Pazol K. A. and M. A. Bloomsmith (1993). **The development of stereotyped body rocking in chimpanzees reared in a variety of nursery settings.** *Animal Welfare* 2(2): 113-129.

Pereira, M. E. (1991). **Primate preference for outdoors.** *Humane Innovations and Alternatives* 5: 313-315.

Pereira, M. E., J. M. Macedonia, D. M. Haring, and E. L. Simons (1989b). **Maintenance of primates in captivity for research: the need for naturalistic environments.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 40-60.

Perkins, L. (1992). **Variables that influence the activity of captive orangutans.** *Zoo Biology* 11(3): 177-186.

Peterson, E. A. (1980). **Noise and laboratory animals.** *Laboratory Animal Science* 30: 422-439.

Peterson, E. A., J. S. Augenstein, C. L. Hazelton, D. Hetrick, R. M. Levene, and D. C. Tanis (1984). **Some cardiovascular effects of noise.** *Journal of Auditory Research* 24(1): 35-62.

Petherick, J. C. and J. Rushen (1997). **Behavioral restriction.** In *Animal Welfare*, M. C. Appleby and B. O. Hughes (eds.) CAB International: New York, pp. 89-105.

Phillips, K. A. (1998). **Tool use in wild capuchin monkeys (*Cebus albifrons trinitatis*).** *American Journal of Primatology* 46(3): 259-261.

Platt, D. M., J. H. Kinsey, M. J. Jorgensen, and M. A. Novak (1996). **Factors affecting the expression of self-injurious behavior in rhesus monkeys *(Macaca mulatta).*** *International Primate Society (IPS) Abstracts* #768.

Platt, D. M. and M. A. Novak (1997). **Videostimulation as enrichment for captive rhesus monkeys (*Macaca mulatta*).** *Applied Animal Behaviour Science* 52: 139-155.

Platt, M. M. and R. L. Thompson (1985). **Mirror responses in a Japanese macaque troop (Arashiyama West).** *Primates* 26: 300-317.

Poole, T. (1987). **Social behavior of a group of orangutans *(Pongo pygmaeus*) on an artificial island in Singapore Zoological Gardens.** *Zoo Biology* 6(4): 315-330.

Poole, T. (1991b). **Criteria for the provision of captive environments.** In *Primate responses to environmental change,* H. O. Box, ed., Chapman and Hall: London, England, pp. 357-374.

Poole, T. (1992). **Nature and evolution of behavioral needs in mammals.** *Animal Welfare* 1(3): 203-220.

Poole, T. (1997a). Personal communication.

Poole, T. (1997b). **Happy animals make good science.** *Lab Animals* 31: 116-124.

Poole, T., P. Costa, W. J. Netto, K. Schwarz, B. Wechsler, and D. Whittaker (1994). **Non-human primates.** In T*he Accommodation of Laboratory Animals in Accordance with Animal Welfare Requirements: Proceedings of an International Workshop Held at the Bundesgesundheitsamt, Berlin, 17-19 May 1993,* O'Donoghue, P. N., editor, Bundesministerium für Ernährung, Landwirtschaft und Forsten: Bonn, Germany, pp. 81-86.

Poole, T. and A. W. Thomas (eds.) (1995). ***European Commission DG-XII, INCO Programme, Primate Vaccine Evaluation Network [PVEN]: Recommendations, Guidelines and Information for Biomedical Research Involving Non-Human Primates with Emphasis on Health Problems of Developing Countries.*** European Commission: Brussels. ISBN 900802222-2-4.

Popovic, A. (1997) Personal communication.

Prince, A. M., J. Goodall, B. Brotman, H. Dienske, H. Schellekens, and J.W. Eichberg (1989). **Appropriate conditions for maintenance of chimpanzees in studies with blood-borne viruses: an epidemiologic and psychosocial perspective.** *Journal of Medical Primatology* 18: 27-42.

Pritchard, T. C., S. Reilly, R. B. Hamilton, and R. Norgren (1994). **Taste preference of old world monkeys: I. non-compliant items previously identified - now corrected A single-bottle preference test.** *Physiology and Behavior* 55(3): 477-481.

Prost, J. H. (1977). **Postural behavior in chimpanzees.** *Yearbook of Physical Anthropology* 20: 454-465.

Pruetz, J. D. and M. A. Bloomsmith (1992). **Comparing two manipulable objects as enrichment for captive chimpanzees.** *Animal Welfare* 1(2): 127-137.

Queyras, A., M. Scolavino, and A. Vitale (1997). **Research and animal welfare needs when studying social learning: the case of a colony of captive common marmosets.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.-27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Ray, J. C. and R. M. Sapolsky (1992). **Styles of male social behavior and their endocrine correlates among high ranking wild baboons.** *American Journal of Primatology* 28(4): 231-250.

Reinhardt, V. (1989). **Evaluation of the long-term effectiveness of two environmental enrichment objects for singly caged rhesus macaques.** *Lab Animal* 18(6): 31-33.

Reinhardt, V. (1991). **Group formation of previously single-caged adult rhesus macaqes for the purpose of environmental enrichment.** *Journal of Experimental Animal Science* 34:110-115.

Reinhardt, V. (1993a). **Enticing non-human primates to forage for their standard biscuit ration.** *Zoo Biology* 12: 307-312.

Reinhardt, V. (1994a). **Pair housing rather than single housing for laboratory rhesus macaques.** *Journal of Medical Primatology* 23:426.431.

Reinhardt, V. (1994b). **Social environment for previously single-caged stumptail macaques.** *Animal Technology* 5: 37-41.

Reinhardt, V. (1997e). **Refining the traditional housing and handling of laboratory rhesus macaques improves scientific methodology.** *Primate Report* 49: 93-113.

Reinhardt, V. (1997a). **Refining the traditional housing and handling of research macaques.** [Monograph online available at http://pantheon.yale.edu/~seelig/pef/new/new.html (December 3, 1997)], 9 p.

Reinhardt, V. (1997b). **Species-adequate housing and handling conditions for old world nonhuman primates kept in research instutions.** In *Comfortable Quarters for Laboratory Animals,* V. Reinhardt, ed., Animal Welfare Institute: Washington, DC., pp. 85-93.

Reinhardt, V. (1997c). **The Wisconsin gnawing stick.** *Animal Welfare Information Center Newsletter* 7(3-4): 11-12.

Reinhardt, V. (1997d). **Training nonhuman primates to cooperate during handling procedures: a review.** *Animal Technology* 48(2): 55-73.

Reinhardt, V., W. D. Hauser, S. G. Eisele, M. Champoux (1987). **Social enrichment with infants of the environment for singly chaged adult rhesus monkeys.** *Zoo Biology* 6: 365-371.

Reinhardt, V., C. Liss, and C. Stevens (1995a). **Restraint methods of laboratory non-human primate: a critical review.** *Animal Welfare* 4(3): 221-238.

Reinhardt, V., C. Liss, and C. Stevens (1995b). **Social housing of previously single-caged macaques: What are the options and the risks?** *Animal Welfare* 4(4): 307-328.

Reinhardt, V., C. Liss, and C. Stevens (1996). **Space requirement stipulations for caged non-human primates in the United States: A critical review.** *Animal Welfare* 5(4): 361-372.

Reite, M., R. Short, C. Seiler, and D. J. Pauley (1981). **Attachment, loss, and separation.** *Journal of Child Psychology, Psychiatry, and Allied Disciplines* 22: 141-169. RJ 499-.56

Reynolds, T.R. (1987). **Stride length and its determinants in humans, early hominids, primates, and mammals.** *American Journal of Physical Anthropology* 72(1): 101-115.Rhine, R. J. and R. L. Cox (1989). **How not to enlarge a stable group of stumptailed macaques *(Macaca arctoides).*** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 255-269.

Ripley, S. (1967). **The leaping of langurs: A problem in the study of locomotor adaptation.** *American Journal of Physical Anthropology* 26:149-170.

Robinson, J. G. and C. H. Janson (1987). **Capuchins, squirrel monkeys, and datelines: socioecological convergence with old world primates.** In *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 69-82.

Rodman, P. S. and J. C. Mitani (1987). **Orangutans: sexual dimorphism in a solitary species.** In *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 146-154.

Rose, M. A. (1994). **Environmental factors likely to impact an animal's well-being.** In *Improving the well-being of animals in the research environment--Proceedings of the conference held at the Marriott Hotel, Sydney, October, 1993,*Baker, R.M., G. Jenkin, and D. J. Mellor (eds.) Australian and New Zealand Council for the Care of Animals in Research and Teaching (ANZCCART), Glen Osmond, Australia, pp. 99-116. ISBN 0 646 181165.

Rosenberg, D. P., L. A. Berke, M. Williams, and J. A. Ferandin (1990). **Using computer games for environmental enrichment of rhesus monkeys in space flight and in the vivarium.** *Laboratory Animal Science* 40(5): 548.

Rosenblum, L. A. (1991). **Subjective and objective factors in assessing psychological well-being in nonhuman primates.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates,* M. A. Novak and A. J. Petto, eds., American Psychological Association: Washington, D.C., pp. 43-49.

Rosenblum, L. A. and M. W. Andrews (1995). **Environmental enrichment and psychological well-being of nonhuman primates.** In *Nonhuman Primates in Biomedical Research, Biology, and Management,* B. T. Bennett, C. R. Abee, and R. Henrickson, eds., Academic Press: New York., pp. 101-112.

Rowe, N. (1996). ***The Pictorial Guide to the Living Primates.*** Pogonias Press: East Hampton, New York, 263 pp.

Roy, M. A., R. H. Wolf, L. N. Martin, S. R. S. Rangan, and W. P. Allen (1978). **Social and reproductive behaviors in surrogate reared squirrel monkeys (*Saimiri sciureus).*** *Laboratory Animal Science* 28: 417-421.

Ruiz, J.C. (1993). **Effects of the cohabitation time on scent marking: Behaviors in heterosexual adult pairs of the golden lion tamarin.** *Primate Report* 37: 15-18.

Rumbaugh, D. M. (1988). **Cage design attenuates display patterns of male chimpazees.** *Zoo Biology* 7: 177-180.

Rumbaugh, D. M., D. Washburn, and E. S. Savage-Rumbaugh (1989). **On the care of captive chimpanzees: Methods of enrichment.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp.357-374.

Sackett, G. P. (1991). **The human model of psychological well-being in primates.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates,* M. A. Novak and A.J. Petto, eds., American Psychological Association: Washington, D.C. pp. 35-42.

Sainsbury, A. W. (1990). **The relationship between between husbandry, behavioural monitoring and disease prevention: examples from a colony of marmosets.** In *Welfare and Science: Proceedings of the fifth symposium of the Federation of European Laboratory Animal Science Associations-8-11 June 1993 Brighton, United Kingdom,* J.Bunyap, ed., Royal Society Press: London.

Salzen, E. A. (1989). **A closed colony of squirrel monkeys for laboratory studies.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed. Noyes Publications: Park Ridge, New Jersey, pp. 115-134.

Sambrook, T. D. and H. M. Buchanan-Smith (1996). **What makes novel objects enriching? A comparison of the qualities of control and complexity.** *Laboratory Primate Newsletter* 35(4): 1-4.

Sambrook, T. D. and H. M. Buchanan-Smith (1997). **Control and complexity in novel object enrichment.** *Animal Welfare* 6(3): 207-216.

Savage-Rumbaugh, E. S. (1986). ***Ape language: From conditioned response to symbol.*** Columbia University Press: New York, 433 p.

Schapiro, S. J. and M. A. Bloomsmith (1995). **Behavioral effects of enrichment on singly-housed, yearling rhesus monkeys: an analysis including three enrichment conditions and a control group.** *American Journal of Primatology* 35: 89-101.

Schapiro, S. J., M. A. Bloomsmith, S. A. Suarez, and L. A. Porter (1996a). **Effects of social and inanimate enrichment on the behavior of yearling rhesus monkeys.** *American Journal of Primatology* 40(3): 247-260.

Schapiro, S. J., M. A. Bloomsmith, S. A. Suarez, and L. M. Porter (1997a). **A comparison of the effects of simple versus complex environmental enrichment on the behaviour of group housed, subadult rhesus macaques.** *Animal Welfare* 6(1): 17-28.

Schapiro, S. J., L. Brent, M. A. Bloomsmith, and W. C. Satterfield (1991). **Enrichment devices for nonhuman primates.** *Laboratory*

Animal Science 41: 22-28.

Schapiro, S. J. and D. Bushong (1994). **Effects of enrichment on veterinary treatment of laboratory rhesus macaques.** *Animal Welfare* 3(1): 25-36.

Schapiro, S. J., D. E. Lee-Parritz, L. L. Taylor, L. Watson, M. A. Bloomsmith, and A. Petto. (1994). **Behavioral management of specific pathogen-free rhesus macaques: group formation, reproduction, and parental competence.** *Laboratory Animal Science* 44(3): 229-234.

Schapiro, S. J., P. N. Nehete, J. E. Perlman, and K. J. Sastry (1997b). **Social housing condition affects cell-mediated immune responses in adult rhesus macaques.** *American Journal of Primatology* 42(2): 147.

Schapiro, S. J., S. A Suarez, L. M. Porter, and M. A. Bloomsmith (1996b). **The effects of different types of feeding enhancements on the behavior of single-caged, yearling rhesus macaques.** *Animal Welfare* 5(2): 129-138.

Schmidt, E. M., G. M. Dold, and J. S. McIntosh (1989). **A perch for primate squeeze cages.** *Laboratory Animal Science.* 32(2): 166-167.

Schoenfeld, D. (1989). **Effects of environmental impoverishment on the social behavior of marmosets *(Callithrix jacchus).*** *American Journal of Primatology* Supplement 1: 45-51.

Scott, L. (1991). **Environmental enrichment for single housed common marmosets.** In *Primate Responses to Environmental Change,* H. O. Box, ed., Chapman and Hall: New York, pp. 265-274.

Scott, L. (1997). **Specific requirements of Callitrichidae species.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Seelig, D. (1998). **Pair housing male *Macaca fasciularis*: a summary**. In *Laboratory Primate Newsletter* 37(3): 14-16.

Segal, E. F. (1989). **Preface.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications, Park Ridge, New Jersey, pp. vii-xv.

Seier, J. V. and P. W. DeLange (1996). **A mobile cage facilitating periodic social contact and exercise for caged adult vervet monkeys.** *Journal of Medical Primatology* 25(1): 64-68.

Shefferly, N., J. Fritz, and S. Howell (1993). **Toys as enrichment for captive juvenile chimpanzees (*Pan troglodytes).*** *Laboratory Primate Newsletter,* 32(2): 7-9.

Shepherdson, D., M. Carman, and N. Bemment (no date). **Lar gibbon duets.** *Environmental Enrichment Report No. 1.,* UFAW and Zoological Society of London: Potters Bar, United Kingdom, 6 p.

Shimoji M., C. L. Bowers, and C. M. Crockett (1993). **Initial response to introduction of of a PVC perch by singly caged *Macaca fascicularis*.** *Laboratory Primate Newsletter* 32(4): 8-11.

Shumaker, R. (1995). **List of browse species used by the National Zoo in Washington, D.C.** In *Primate-Talk (internet listserv),* Wisconsin Regional Primate Center, Madison, Wisconsin, date unknown, cited 1995.

Simpson, M. J. A. (1985). **Effects of early experience on the behavior of yearling rhesus monkeys (*Macaca mulatta*) in the presence of a strange object: classification and correlation approaches.** *Primates* 26: 57-72.

Snowdon, C. T. (1991). **Naturalistic environments and psychological well-being.** In *Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates,* M. A. Novak and A.J. Petto, eds., American Psychological Association: Washington, D.C., pp.103-115.

Snowdon, C. T. and A. Savage (1989). **Psychological well-being of captive primates: General considerations and examples from callitrichids.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, NJ, pp.75-88.

Southwick, C. (1967). **An experimental study of intragroup agonistic behavior in rhesus monkeys.** *Behavior* 28: 182-209.

Spijkerman, R. P., H. Dienske, J. A. R. A. M. Van Hooff, and W. Jens (1994). **Causes of body rocking in chimpanzees.** *Animal Welfare* 3(3):193-211.

Spring, S.E., J.O. Clifford, and D. L. Tomko (1997). **Effects of environmental enrichment devices on behaviors of single and group-housed squirrel monkeys.** *Contemporary Topics in Laboratory Animal Science* 36(3): 72-75.

Starin, E. D. (1990). **Object manipulation by wild red colobus monkeys living in the Abuko Nature Reserve, the Gambia.** *Primates* 31(3): 385-391.

Stafford, B. J., A. L. Rosenberger, and B. B. Beck (1994). **Locomotion of free-ranging golden lion tamarins at the National Zoological Park.** *Zoo Biology* 13: 333-344.

Steen, Z. (1995). **Effects of enriched food acquired on activity budgets of two tamarin species at Adelaide Zoo.** *International Zoo News* 42(5): 284-298.

Stegenga, L. (1993). **Modifying spider monkey behavior with the use of environmental variables.** *Shape of Enrichment* 2(3): 3-4.

Struthers, E. J., H. Harvey, and S. Walden (1997). **Utilization of a sensory diet approach for enrichment and mitigation of abnormal behaviors in captive chimpanzees (*Pan troglodytes*).** *American Journal of Primatology* 42(2): 151.

Suarez, S. (1995). **Chimp platforms in outdoor enclosures.** *The Shape of Enrichment* 4(4): 5-6.

Sugiyama, Y. (1995). **Drinking tools of wild chimpanzees at Bossou.** *American Journal of Primatology* 37: 263-269.

Suomi, S. J. (1986). **Behavioral aspects of successful reproduction in primates.** In *Primates: the road to self-sustaining populations.* K. Benirschke, ed., Springer-Verlag: New York, pp.331-340.

Suomi, S. J. (1987). **Genetic and maternal contributions to individual differences in rhesus monkey biobehavioral development.** In *Perinatal Development: A Psychobiological Perspective,* N. Krasnegor, E. Blass, M. Hofer, and W. Smotherman, eds., Academic Press: New York, pp.397-420**.**

Suomi, S. J., C. D. Eisele, S. A. Grady, and H. F. Harlow (1975). **Depressive behavior in adult monkeys following separation from family environment.** *Journal of Abnormal Psychology* 84: 576-578.

Suomi, S. J. and M. J. Novak (1991). **The role of individual differences in promoting psychological well-being in rhesus monkeys.** In *Through the Looking Glass: Issues of Psychological Well-Being in Captive Nonhuman Primates,* M. A. Novak and A.J. Petto, eds., American Psychological Association: Washington, D. C., pp. 57-65.

Suomi, S. J., J. M. Scanlan, K. L. R. Rasmussen, M. Davidson, S. Boinski, J. D. Higley, and B. Marriot (1989). **Pituitary-adrenal response to capture in Cayo-derived M-troop rhesus monkeys.** *Puerto Rico Health Sciences Journal* 8: 171-176.

Suzuki, A., (1965). **An ecological study of wild Japanese monkeys in snowy areas, focused on their food habits.** *Primates* 6: 31-72.

Taff, M. A. and P. Dolhinow (1989). **Langur monkeys (*Presbytis entellus)* in captivity.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates*. E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 291-304.

Taira, K., and E. T. Rolls (1996). **Receiving grooming as a reinforcer for the monkey.** *Physiology and Behavior* 59(6): 1189-1192.

Tardif, S., K. Hyde, and L. Digby (1994). **Evidence for suppression of ovulation in singly-housed female common marmosets (*Calithrix jacchus).*** *Laboratory Primate Newsletter* 33(2): 2-6.

Taylor, W. J., D. A. Brown, W. L. Davis, and M. L. Laudenslager (1997). **Novelty influences use of play structures by a group of socially housed bonnet macaques.** *Laboratory Primate Newsletter* 36(1): 4-6.

Taylor, W. J., D. A. Brown, R. L Richardson, and M. L. Laudenslager (1998). **The effect of individual housing on social behavior of adult male bonnet macaques.** In *Contemporary Topics in Laboratory Animal Science* 37(3): 47-50.

Taylor, W. J. and M. L. Laudenslager (1998). **Low-cost environmental enrichment plan for laboratory macaques.** *Lab Animal* 27(4): 28-31.

Thomas, W. D. and E. J. Maruska (1996). **Mixed-species exhibits with mammals.** In *Wild Mammals in Captivity: Principles and Techniques,* D. G. Kleiman, M. E. Allen, K. V. Thomson, and S. Lumpkin, eds., University of Chicago Press: Chicago, Illinois, pp.204-211.

Thompson, K. V. (1996). **Chapter 34: Behavioral development and play.** In *Wild Mammals in Captivity: Principles and Techniques,* D.G . Kleiman, M. E. Allen, K. V. Thomson, and S. Lumpkin, eds., University of Chicago Press: Chicago, Illinois, pp. 352-371.

Thorington, L. (1985). **Spectral irradiance and temporal aspects of natural and artificial light.** In *The medical and biological affects of light.* R. J. Wurtman, M. J. Baum, and J. T. Potts, eds., New York Academy of Sciences: New York, pp. 28-54.

Toates, F. (1995). ***Stress: conceptual and biological aspects*.** John Wiley and Sons, Ltd.: New York.

Tolan, J. C., D. R. Malone, and C. M. Rogers (1980). **An exercise cage for monkeys.** *Laboratory Primate Newsletter* 19(1): 3-5.

Tomasello, M. and J. Call, (eds.) (1997). ***Primate cognition.***Oxford University Press: New York, 517 p.

Traylor-Holzer, K. and P. Fritz (1985). **Utilization of space by adult and juvenile groups of captive *c*himpanzees *(Pan troglodytes).*** *Zoo Biology* 4(2): 115-127.

Tripp, J. K. (1985). **Increasing activity in captive orangutans: Provisions of manipulable and edible materials.** *Zoo Biology* 4(3): 225-234.

Turkkan, J. S., N. A. Ator, J. V. Brady, and K. A. Craven (1989). **Beyond chronic catheterization in laboratory primates.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates*, E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 305-322.

Turnquist, J. (1983). **Influence of age, sex, and caging on joint mobility in the patas monkey.** *American Journal of Physical Anthropology* 61(2): 211-220.

Turnquist, J. (1985). **Passive joint mobility in patas monkeys: Rehabilitation of caged animals after release into a free-ranging environment.** *American Journal of Physical Anthropology* 67(1): 1-6.

Tustin, G. W., L. E. Williams, and A. G. Brady (1996). **Rotational use of a recreational cage for the environmental enrichment of Japanese macaques.** *Laboratory Primate Newsletter* 35(1): 5-7.

Tuttle, R. H. (1986). ***Apes of the world: Their Social Behavior, Communication, Mentality, and Ecology.*** Noyes Publication: Park Ridge, New Jersey, 421 p.

U. S. Department of Agriculture, Animal and Plant Health Inspection Service (1998). *Title 9, Animal and Animal Products, Part 3, Standards, Subpart D, Specifications for the Humane Handling, Care, Treatment, and Transportation of Nonhuman Primates*, **Section 3.81, Environmental enhancement to promote psychological well-being**. 9 CFR 3.81.

U. S. Department of Agriculture, Animal and Plant Health Inspection Service, Animal Care (1996). ***USDA Employee Opinions on the Effectiveness of Performance-Based Standards for Animal Care Facilities*.** USDA, APHIS: Riverdale, Maryland, December, 1996.

Van Lawick-Goodall, J. (1968). **The behaviour of free-living chimpanzees in the Gombe stream reserve.** *Animal Behaviour Monographs* 3 (1): 161-311.

Van Roosmalen, M. G. M., and L. L. Klein (1988). **The spider monkey, genus *Ateles.*** In *Ecology and Behavior of Neotropical Primates, Vol. 2*, Mittermeier, R. A., A. B. Rylands, A. F. Coimbra-Filho, and G. A. B. De Fonseca, eds., World Wildlife Fund, Washington, DC., pp. 455-538.

Van Schaik, C. and J. A. R. A. M. Van Hooff (1996). **Toward an understanding of the oragutan's social system.** In *Great ape societies*, W. C. McGrew, L. Marchant, and T. Nishida, eds., Cambridge University Press: Cambridge, United Kingdom, pp.3-15.

Van Schaik C., M. A. Van Nordwijk, T. Van Bragt, M. A. Blankenstein (1991). **A pilot study of the social correlates of levels of**

urinary levels of cortisol, prolactin, and testosterone in wild long-tailed macaques. *Primates* 32: 345-356.

Van Vlissingen, J. M. F. (1997) **Welfare implications in biomedical research.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Veasey, J. S., N. K. Waron, and R. J. Young (1996). **On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator.** *Animal Welfare* 5(1): 13-24.

Vermeer, J. (1994). **Browsing, a garden of enrichment.** *Shape of Enrichment* 3(4): 10-11.

Vermeer, J. (1997). **The formation of a captive squirrel monkey group.** *International Zoo News* 44: 146-149.

Visalberghi, E. (1990). **Tool use in *Cebus*.** *Folia Primatologica* 54:146-154.

Visalberghi, E. and J. R. Anderson (1993). **Reasons and risks associated with manipulating captive primates' social environments.** *Animal Welfare* 2(1): 3-15.

Walsh, S., C. A. Bramblett, and P. L. Alford (1982). **A vocabulary of abnormal behaviors in restrictively reared chimpanzees.** *American Journal of Primatology* 3: 315-319.

Walters, J. F. (1987). **Transition to Adulthood.** In *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 358-369.

Washburn, D. A. and D. M. Rumbaugh (1991). **Impaired performance from brief social isolation of rhesus monkeys *(Macaca mulatta)*: A multiple video task assessment.**

Wassel, K. and S. Race (1994). **Tamarin enrichment at the Utica Zoo.** *The Shape of Enrichment* 3(1): 1-2.

Watson, C. (1997). **Getting serious about monkey business.** *Science and Animal Care* 8(2): 1-3.

Watson, L. M., D. E. Lee-Parritz, A. J. Petto, M. N. La Rean-Alves (1995). **Effect of social rearing conditions on affiliative and reproductive behaviors of adult primate multifemale grouped rhesus macaques: a case study.** In *Contemporary Topics in Laboratory Animal Science* 34(6): 66-69.

Watson, S. L. and C. A. Shively (1996). **Effects of cage configuration on behavior of cynomologous macaques.** *International Primate Society/American Society of Primatologists Congress Abstract No. 674.* IPS Congress Abstracts, Madison, Wisconsin.

Watts, E. and A. Meder (1996). **Introduction and socialization techniques for primates.** In *Wild Mammals in Captivity: Principles and Techniques.* D.G. Kleiman, M. E. Allen, K.V. Thomson, and S. Lumpkin, eds., University of Chicago Press: Chicago, Illinois, pp. 67-77.

Watts, D. P. and A. E. Pusey (1993). **Behavior of juvenile and adolescent great apes.** In *Juvenile primates: life history, development, and behavior,* Pereira, M. E. and L. F. Fairbanks, eds. Oxford University Press: New York. Chapter 11, pp. 148-172.

Weed J. L., Baker, S. C. Harbaugh, and J. Erwin (1995). **Innovative enclosures for laboratory primates: evaluation of a "breeding condominium".** *Lab Animal* 24(7): 28-32.

Wemelsfelder, F. (1985). **Animal boredom: Is a scientific study of the subjective experiences of animals possible?** In *Advances in Animal Welfare Science,* M.W. Fox and L. D. Mickley, eds., Martinus Nijhoff: Boston, pp. 115-154.

Wemelsfelder, F. (1993). **The concept of animal boredom and its relationship to stereotyped behaviour.** In *Stereotypic Animal Behaviour: Fundamentals and Applications to Animal Welfare*, A. B. Lawrence and J. Rushen, eds., CAB International, United Kingdom, pp. 65-96.

Westergaard, G. C. and D. Munkenbeck-Fragaszy (1985). **Effects of manipulatable objects on the activity of captive capuchin monkeys (*Cebus apella*).** *Zoo Biology* 4(4): 317-327.

Westergaard, G. C. and T. Lindquist (1987). **Manipulation of objects in a captive group of lion-tailed macaques *(Macaca***

silenus). *American Journal of Primatology* 12: 231-234.

Whitney, R. A. and E. J. Wickings (1987). **Macaques and other old world simians.** In *UFAW handbook on the care and management of laboratory animals, 6th edition,* T. S. Poole, ed., Longman Scientific and Technical: Essex, England, pp.599-627.

Williams, L. E. and C. R. Abee (1988). **Aggression with mixed age-sex groups of Bolivian squirrel monkeys following single animal introductions and new group formations.** *Zoo Biology* 7(2): 139-145.

Williams, L. E., C. R. Abee, S.R . Barnes, and R. B. Ricker (1988). **Cage design and configuration for an arboreal species of primate.** *Laboratory Animal Science* 38(3): 289-251.

Williams, L. E. and I. S. Bernstein (1995). **Study of primate social behavior.** In *Nonhuman Primates in Biomedical Research, Biology, and Management.* B.T. Bennett, C. R. Abee, and R. Henrickson, eds., Academic Press: New York, pp. 77-100.

Wilson, C. C. (1972). **Spatial factors and the behavior of nonhuman primates.** *Folia Primatologoca* 18: 256-275.

Wilson, S. F. (1982). **Environmental influences on the activity of captive apes.** *Zoo Biology* 1(3): 201-209.

Wilson, S. G. (1982). **Environmental influences on the activity of captive great apes.** *Zoo Biology* 1(3): 201-209.

Wolff, A. and G. Ruppert (1991). **A practical assessment of a non-human primate exercise program.** *Lab Animal* 20(2): 36-39.

Woodbeck, T. and V. Reinhardt (1991). **Perch use by *Macaca mulatta* in relation to cage location.** *Laboratory Primate Newsletter* 30(4): 11-12.

Woolley, A. P. A. H. (1997). **Requirements of biomedical research in terms of housing and husbandry: pharmacology and toxicology.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Worlein, J. M. and G. S. Sackett (1997). **Social development in nursery-reared pigtailed macaques *(Macaca nemestrina).*** *American Journal of Primatology* 41: 23-35.

Wrangham, R. W. (1977). **Feeding behavior of chimpanzees in Gombe National Park, Tanzania.** In *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys, and apes,* T. H. Clutton-Brock, ed., Academic Press: New York, pp.503-538.

Wrangham, R. W. (1983). **Social relationships in comparative perspective.** In *Primate Social Relationships: An Integrated Approach,* R..H. Hinde, ed., Blackwell Scientific: Oxford, United Kingdom, pp.255-62.

Wright, P., D. Haring, M. Izard, and E. Simons (1989). **Psychological well-being of nocturnal primates in captivity.** In *Housing, Care and Psychological Well-being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 61-65.

Young, N., E. J. Struthers, and P. A. Frost (1996). **#696 The effect of social housing configuration on the direction of affiliative initiations in chimpanzee (Pan troglodytes) mother-infant dyads.** In *Abstracts from the XVIth Congress of the International Primate Society and the XIXth Conference of the American Society of Primatologists: August 11-16, 1996, University of Wisconsin-Madison,* Coulston Foundation and New Mexico State University, Holloman AFB, NM 88330.

Zeller, A.C. (1987). **Communication by sight and smell.** In *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp. 433-439.

Zimmerman, E., P. Zimmerman, and A. Zimmerman (1980). **Vergleich einiger Kommunikationsformen fnf nonhumaner primatenarten.** *Zeitschrift des Klner Zoo* (23): pp. 3-20.

B. Other Sources

Alexander, R. M. and Maloiy, G. M. O. (1984). **Stride lengths and stride frequency of primates.** *Journal of Zoology* 202(4): 577-582.

Anderson, J. R., André, E., and Wolf, P. (1995). **Successful mother and group rearing of a newborn capuchin monkey (*C.***

capucinus) **following emergency major surgery.** *Animal Welfare* 4(3): 171-182.

Baker, K. C. and Aureli, F. (1996). **The neighbor effect: Other groups influence intragroup agonistic behavior in captive chimpanzees.** *American Journal of Primatology* 40(3): 283-291.

Baxter, M. R. (1983). **Ethology in environmental design for animal production.** *Applied Animal Ethology* 9(3-4): 207-220.

Bayne, K. A. L. and S. Dexter (1992a). **Removing an environmental enrichment device can result in a rebound of abnormal behavior in rhesus monkeys.** *American Journal of Primatology* 27: 15. Abstract.

Benirschke, K. (ed.) (1986). ***Primates: the road to self-sustaining populations.*** Springer-Verlag: New York, 1044 p.

Bennett, B. T., C. R. Abee, and R. Henrickson, eds. (1995). ***Nonhuman Primates in Biomedical Research: Biology and Management,*** Academic Press: New York, 428 p.

Bielitzki, J., T. G. Susor, K. Elias, and D. M. Boeden (1990). **Improved cage design for single housing of social nonhuman animals.** *Laboratory Animal Science* 40(4): 428-431.

Bloomsmith, M. A. (1989b). **Interactions between adult male and immature captive chimpanzees: implications for housing chimpanzees.** *American Journal of Primatology* Supplement 1: 93-99.

Boccia, M. L., M. Reite, K. Kaemingk, D. Held, and M. L. Laudenslager (1989). **Behavioral and autonomic responses to peer separation in pigtail macaque monkey infants.** *Developmental Psychobiology* 22:447-461

Chamove, A. S. (1989). **Enrichment in chimpanzees: unpredictable ropes and tolls.** *Journal of the Association of British Wild Animal Keepers* 16: 139-141.

Clarke, M. R. and J. L. Blanchard (1994). **All-male social group formation: Does cutting canine teeth promote social integration?** *Laboratory Primate Newsletter* 33(2): 5-9.

Coe, C. L., S. G. Wiener, and S. Levine (1983). **Psychoendocrine responses of mother and infant monkeys to disturbance and separation.** In *Symbiosis in Parent-Young Interactions.* L. A. Rosenblum and H. Meltz, eds., Plenum Press: New York, pp. 189-214.

Coe, C. L., S. G. Wiener, L. T. Rosenberg, and S. L. Levine (1985). **Physiological consequences of maternal separation and loss in the squirrel monkey.** In *Handbook of squirrel monkey research.* L. A. Rosenblum and Christopher L. Coe, eds. Plenum Press: New York, pp. 127-168.

Deputte, B. L. (1997). **The ethologist's view.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Dettmer, E. L., K. A. Phillips, D. R. Rager, I. S. Bernstein, and D. M. Fragaszy (1996). **Behavioral and cortisol responses to repeated captive and venipuncture in *C. apella.*** *American Journal of Primatology* 38(4): 357-362.

Erwin, J. and R. Deni (1979). **Strangers in a strange land.** In *Captivity and behavior: primates in breeding colonies, laboratories, and zoos,* J. Erwin, T. Maple, and G. Mitchell, eds., Van Nostrand Reinhold: New York, pp.1-28.

European Association of Zoos and Aquaria (EAZA) (1994). ***EAZA Standards for the Accommodation and Care of Animals in Zoos. 18/06/94***. EAZA Executive Office, P. O. Box 20164, 1000 HD Amsterdam, The Netherlands. [Address from http://www.worldzoo.org/eaza, January 10, 1999.]

Feistner, A. T. C. and A. S. Chamove (1986). **High motivation toward food increases food-sharing in cotton-top tamarins.** *Developmental Psychobiology* 19(5): 439-452.

Fleagle, J. (1974). **Dynamics of a brachiating siamang.** *Nature* 248: 259-260.

Fraser, D., D. M. Weary, E. A. Pajor, and B. N. Milligan (1997). **A scientific conception of animal welfare that reflects ethical concerns.** *Animal Welfare* 6(3): 187-205.

Fraser, A. F. (1989). **Welfare and well-being.** *Veterinary Record* 125(12): 332.

Fritz, P. and J. Fritz (1979). **Resocialization of chimpanzees: Ten years' of experience at the Primate Foundation of Arizona.** *Journal of Medical Primatology* 8(4): 202-221.

Gillin, A. G. (1994). **Group housing of the hamadryas baboon (*Papio hamadryas*)--the NHMRC-sponsored baboon colony.** In *Improving the well-being of animals in the research environment--Proceedings of the conference held at the Marriott Hotel, Sydney, October, 1993,* Baker, R.M., G. Jenkin, and D. J. Mellor (eds.), Australian and New Zealand Council for the Care of Animals in Research and Teaching (ANZCCART), Glen Osmond, Australia, pp. 117-118. ISBN 0 646 181165.

Goosen, C. (1981). **Abnormal behavior patterns in rhesus monkeys: symptoms of mental disease?** *Biological Psychiatry* 16: 697-716.

Harlow, H. F. and M. K. Harlow (1969). **Effects of various mother-infant relationships in rhesus monkey behaviors.** In *Determinants of Infant Behavior, Vol. 4,* B. M. Foss, ed., Methuen: London, pp.15-36.

Harvey, P. H., R. D. Martin, and T. H. Clutton-Brock (1987). **Life histories in comparative perspective.** In *Primate Societies,* B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press: Chicago, Illinois, pp.358-369.

Hughes, B. O. and I. J. H. Duncan (1988). **The notion of ethological "need", models of motivation and animal welfare.** *Animal Behaviour* 36: 1967-1707.

Jenkins, F. A., ed. (1974). ***Primate locomotion.*** Academy Press: New York, New York, 390 p.

Jones, B. (1996). ***Current Standards in Europe for the Care of Non-human Primates.*** Research Animals Department, Royal Society for the Prevention of Cruelty to Animals, West Sussex, United Kingdom.

Kerl, J. (1997). **Measuring psychological well-being: A methodological approach using heart rate telemetry, space utilization, and behavioral time budgets in common marmosets.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Kessel, A.L. and L. Brent (1995b). **An activity cage for baboons, Part II, Long-term effects and management issues.** *Contemporary Topics in Laboratory Animal Science* 34(6): 80-83.

Lawrence, A. B. and J.Rushen, (eds.) (1993). ***Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*.** CAB International: Wallingford, United Kingdom, 212 p.

Line, S. W. (1995). **Effects of observation techniques on the behavior of adult rhesus macaques.** *Contemporary Topics* 34(6): 61-65.

Luttrell, L., L. Acker, M. Urben, and V. Reinhardt (1997). **Training a large troop of rhesus macaques to cooperate during catching: Analysis of the time investment.** *Animal Welfare* 3(2): 135-140.

Manser, C. (1992). ***Assessment of stress in laboratory animals*.** Royal Society for the Prevention of Cruelty to Animals (RSPCA): London, England, 208 p.

Maple, T. L. and M.P. Hoff (1982). **Sex and age differences in the avoidance of reptile exhibits by zoo visitors.** *Zoo Biology* 1(3): 263-269.

Mason, W. A. (1963). **The effects of environmental relocation in the social development of rhesus monkeys.** In *Primate Social Behavior,* C.H. Southwick, ed., Van Nostrand: New York, pp. 161-163.

Matthews, L. R. (1994). **A new methodology for assessing the behavioural requirements of captive animals.** In *Improving the well-being of animals in the research environment--Proceedings of the conference held at the Marriott Hotel, Sydney, October, 199,.*Baker, R.M., G. Jenkin, and D. J. Mellor (eds.), Australian and New Zealand Council for the Care of Animals in Research and Teaching (ANZCCART), Glen Osmond, Australia, pp. 143-146. ISBN 0 646 181165.

McGraw, W. Scott (1988). **Posture and support use of Old World monkeys (Cercopithecidae): The influence of foraging strategies, activity patterns, and the spatial distribution of preferred food items.** *American Journal of Primatology* 46(3): 229-250.

Miller, L. C., K. A. Bard, C. J. Juno, R. D. Nadler (1986). **Behavioral responsiveness of young chimpanzees (*Pan troglodytes)* to a novel environment**. *Folia primatologica* 47: 128-142.

Mittermeier, R. A., I. Tattsersall, W. R. Konstant, D. M. Meyers, and R. B. Mast (1994). ***Lemurs of Madagascar. Conservation International Tropical Field Guide Series 1.*** Conservation International: Washington, D.C., 356 p.

National Health and Medical Research Council Animal Welfare Committee [of Australia] 1997. ***Policy on the use of non-human primates in medical research.*** Available on: http://www.health.gov.au:80/nhmrc/research/awc/nonhuman.htm on December 11, 1998.

Nevison, C. M., F. D. G. Rayment, M. J. A. Simpson (1996). **Birth sex ratios and maternal social rank in a captive colony of rhesus monkeys (*Macaca mulatta)*.** *American Journal of Primatology* 39(2): 123-138.

Nishida, T., R. W. Wrangham, J. Goodall, and S. Uehara (1983). **Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania.** *Journal of Human Evolution* 12: 467-480.

Novak, M. A. and A. J. Petto, (eds.) (1991a). ***Through the Looking Glass: Issues of Psychological Well-Being In Captive Nonhuman Primates*.** American Psychological Association: Washington, D.C., 285 p.

Pereira, M. E., J. M. Macedonia, D. M. Haring, and E. L. Simons (1989a). **Feeding enrichment for captive great apes.** In *Housing, Care, and Psychological Well Being of Captive and Laboratory Primates,* E. F. Segal, ed., Noyes Publications: Park Ridge, New Jersey, pp. 45-51.

Poole, T. (1988a). **Behaviour, housing and welfare of non-human primates.** In *New Developments in Biosciences: Their Implications for Laboratory Animal Science,* A.C. Beynen and H.A. Solleveld, eds., Kluwer-Nijhoff Publishers: Dordrecht, The Netherlands, pp.231-237.

Poole, T. (1988b). **Normal and abnormal behaviour in captive primates.** *Primate Report* 22: 3-12.

Poole, T. (1991a). **The behavioural needs of captive primates: can they be identified?** In Ehara, A., Kimura, T., Takenaka, O., and Iwamoto, M., eds., *Primatology Today: Proceedings of the XIIth Congress of the International Primatological Society, Nagoya and Kyoto, July, 1990*, pp. 659-664. Elsevier Science Publishers, New York.

Poole, T. (1998). **Chapter 6: Meeting a mammal's psychological needs.** In *Second nature: environmental enrichment for captive animals,* Shepherdson, O. J., J. D. Melton, and M. Hutchins, eds., Smithsonian Institution Press: Washington, D.C., pp. 83-94.

Poole, T. and R. Hubrecht (1994). **Letter to the editor.** *Lab Animal* 23(7): 51.

Reinhardt, V. (1993b). **Using the mesh ceiling in a food puzzle to encourage foraging behavior in caged rhesus macaques.** *Animal Welfare* 2(2): 165-172.

Reinhardt, V. (1994). **Continuous pair-housing of caged *Macaca mulatta*: Risk evaluation.** *Laboratory Primate Newsletter* 33(1): 1-4.

Reinhardt, V. and A. Roberts (1997). **Effective feeding enrichment for non-human primates: a brief review.** *Animal Welfare* 6(3): 265-272.

Reite, M. (1977). **Maternal separation in monkey infants: A model of depression.** In *Animal Models in Psychiatry and Neurology.* I. H. Usdin and E. Usdin, eds., Pergamon Press: Elmsford, N.Y., pp. 127-140.

Reite, M., K. Kaemingle, and M. Boccia (1989). **Maternal separation in bonnet monkey infants: Altered attachment and social support.** *Child Development* 60: 473-481.

Schapiro, S. J., M. A. Bloomsmith, A. . Kessel, and C. A. Shively (1993). **Effects of enrichment and housing on cortisol response in juvenile rhesus monkeys.** *Applied Animal Behaviour Science* 37(3): 215-263.

Schapiro, S. J., M. A. Bloomsmith, L. M. Porter, and S. A. Suarez (1996c). **Enrichment effects on rhesus monkeys successfully housed singly, in pairs, and in groups.** *Applied Animal Behaviour Science* 48(3-4): 159-172.

Schnell, C. R. and P. Gerber (1997). **Training and monitoring of animals.** In *Abstracts of the Second EUPREN/EMRG Winter*

Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Schrier, A. M. and F. Stollnitz, (eds.) (1971). ***Behavior of Nonhuman Primates: Modern Research Trends, Vol 3,*** Academic Press: New York, 206 pp.

Scott, L. (1990). **Training non-human primates--meeting their behavioral needs.** In *Animal Training: A Review and Commentary on Current Practice, Proceedings of a symposium organized by Universities Federation for Animal Welfare at the University of Cambridge, 26-27 Sept. 1989,* UFAW, London, UK, pp. 129-133.

Smuts, B. B., D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, (eds.) (1987). ***Primate Societies,*** University of Chicago Press: Chicago, Illinois, 578 p.

U. S. Department of Agriculture, Animal and Plant Health Inspection Service (1989). **Animal Welfare: Standards; Proposed Rule (9 C.F.R., Part 3) (APHIS Docket No. 87-004).** *Federal Register* 54:10897-10954; March 15, 1989.

U. S. Department of Agriculture, Animal and Plant Health Inspection Service (1990). **Animal Welfare: Standards; Proposed Rule (9 C.F.R., Part 3) (APHIS Docket No. 90-040).** *Federal Register* 55:33448-33531; August 15, 1990. See especially pp. 33490-33499, 33503, and 33525-33526.

U. S. Department of Agriculture, Animal and Plant Health Inspection Service (1991). **Animal Welfare: Standards; Final Rule (9 C.F.R., Part 3)**, *Federal Register* 56:6495--6505.

Van Hooff, J. A. R. A. M. (1997). **Primatological research in Europe: The academic world.** In *Abstracts of the Second EUPREN/EMRG Winter Workshop : The housing of non-human primates used for experimental and other scientific purposes: Issues for consideration, Rome 27.09.1996*. [Monograph online available from: http://www.dpz.gwdg.de:80/eupren/eupren.htm (March 23, 1998)]. European Primate Resources Network (EUPREN).

Virgin, C. E. and R. Sapolsky (1997). **Styles of male social behavior and their endocrine correlates among low ranking baboons.** *American Journal of Primatology* 42(1): 25-39.

Watson, D. S. B. (1991). **A built-in perch for primate squeeze cage.** *Laboratory Animal Science* 41:378-379.

Watson, S., J. Ward, K. Izard, and D. Stafford (1996). **An analysis of birth sex ratio bias in captive prosimian species.** *American Journal of Primatology* 38(4): 357-362.

Whitehead, J. M. (1986). **Development of feeding selectivity in mantled howling monkeys (*Alouatta palliata).*** In *Primate ontogeny, cognition and social behavior,* J.G. Else and P.C. Lee, eds., Cambridge University Press: New York, pp.105-117.

Wilson, E. O. (1975). ***Sociobiology: the new synthesis.***Cambridge University Press: New York, 697 p.

Wood, W. (1997). **Changes in grooming and play behavior across three levels of environmental complexity in an intensively housed group of zoo chimpanzees.** *American Journal of Primatology* 42(2): 156.

Zoo Licensing Act of 1981. ***The Secretary of State's Standards of Modern Zoo Practice.*** United Kingdom.

APPENDIX A. 9 CFR Section 3.81

Environment Enhancement to Promote Psychological Well-Being of Nonhuman Primates

CHAPTER I--ANIMAL AND PLANT HEALTH INSPECTION SERVICE, DEPARTMENT OF AGRICULTURE

PART 3--STANDARDS--Table of Contents

Subpart D--Specifications for the Humane Handling, Care, Treatment, and Transportation of Nonhuman Primates

Sec. 3.81 Environment enhancement to promote psychological well-being.

Dealers, exhibitors, and research facilities must develop, document, and follow an appropriate plan for environment enhancement

adequate to promote the psychological well-being of nonhuman primates. The plan must be in accordance with the currently accepted professional standards as cited in appropriate professional journals or reference guides, and as directed by the attending veterinarian. This plan must be made available to APHIS upon request, and, in the case of research facilities, to officials of any pertinent funding agency. The plan, at a minimum, must address each of the following:

(a) Social grouping. The environment enhancement plan must include specific provisions to address the social needs of nonhuman primates of species known to exist in social groups in nature. Such specific provisions must be in accordance with currently accepted professional standards, as cited in appropriate professional journals or reference guides, and as directed by the attending veterinarian. The plan may provide for the following exceptions:

(1) If a nonhuman primate exhibits vicious or overly aggressive behavior, or is debilitated as a result of age or other conditions (e.g., arthritis), it should be housed separately;

(2) Nonhuman primates that have or are suspected of having a contagious disease must be isolated from healthy animals in the colony as directed by the attending veterinarian. When an entire group or room of nonhuman primates is known to have or believed to be exposed to an infectious agent, the group may be kept intact during the process of diagnosis, treatment, and control.

(3) Nonhuman primates may not be housed with other species of primates or animals unless they are compatible, do not prevent access to food, water, or shelter by individual animals. and are not known to be hazardous to the health and well-being of each other. Compatibility of nonhuman primates must be determined in accordance with generally accepted professional practices and actual observations, as directed by the attending veterinarian, to ensure that the nonhuman primates are in fact compatible. Individually housed nonhuman primates must be able to see and hear nonhuman primates of their own or compatible species unless the attending veterinarian determines that it would endanger their health, safety, or well-being.

(b) Environmental enrichment. The physical environment in the primary enclosures must be enriched by providing means of expressing noninjurious species-typical activities. Species differences should be considered when determining the type or methods of enrichment. Examples of environmental enrichments include providing perches, swings, mirrors, and other increased cage complexities; providing objects to manipulate; varied food items; using foraging or task-oriented feeding methods; and providing interaction with the care giver or other familiar and knowledgeable person consistent with personnel safety precautions.

(c) Special considerations. Certain nonhuman primates must be provided special attention regarding enhancement of their environment, based on the needs of the individual species and in accordance with the instructions of the attending veterinarian. Nonhuman primates requiring special attention are the following:

(1) Infants and young juveniles;

(2) Those that show signs of being in psychological distress through behavior or appearance;

(3) Those used in research for which the Committee-approved protocol requires restricted activity;

(4) Individually housed nonhuman primates that are unable to see and hear nonhuman primates of their own or compatible species; and

(5) Great apes weighing over 110 lbs. (50 kg). Dealers, exhibitors, and research facilities must include in the environment enhancement plan special provisions for great apes weighing over 110 lbs. (50 kg), including additional opportunities to express species-typical behavior.

(d) Restraint devices. Nonhuman primates must not be maintained in restraint devices unless required for health reasons as determined by the attending veterinarian or by a research proposal approved by the Committee at research facilities. Maintenance under such restraint must be for the shortest period possible. In instances where long-term (more than 12 hours) restraint is required, the nonhuman primate must be provided the opportunity daily for unrestrained activity for at least one continuous hour during the period of restraint, unless continuous restraint is required by the research proposal approved by the Committee at research facilities.

(e) Exemptions. (1) The attending veterinarian may exempt an individual nonhuman primate from participation in the environment enhancement plan because of its health or condition, or in consideration of its well-being. The basis of the exemption must be recorded by the attending veterinarian for each exempted nonhuman primate. Unless the basis for the exemption is a permanent condition, the exemption must be reviewed at least every 30 days by the attending veterinarian.

(2) For a research facility, the Committee may exempt an individual nonhuman primate from participation in some or all of the otherwise required environment enhancement plans for scientific reasons set forth in the research proposal. The basis of the

exemption shall be documented in the approved proposal and must be reviewed at appropriate intervals as determined by the Committee, but not less than annually.

(3) Records of any exemptions must be maintained by the dealer, exhibitor, or research facility and must be made available to USDA officials or officials of any pertinent funding Federal agency upon request.

(Approved by the Office of Management and Budget under control number 0579-0093)

APPENDIX B. Glossary*

* See Rowe (1996) for definitions and descriptions of terms relating to types of primates such as: bonobos, callitrichids, cynomologous, guenons, hamadryas, mangabeys, patas, prosimians, tarsiers.

9 CFR--the ninth volume of the Code of Federal Regulations which contains the regulations implementing the Animal Welfare Act. The part of them that deals with environment enhancement to promote psychological well-being of nonhuman primates is 9CFR3.81.

affiliative--close, friendly social relations

agonism--aggressive or defensive social interaction (such as fighting or fleeing) between individuals

arboreal--inhabiting or frequenting trees

allomothering--care of an infant by a group member other than its mother (similar to babysitting)

alloparenting--care of an infant by a group member other than its parent (similar to babysitting)

antihepatotoxic--counteracting substances that damage the liver or preventing damage to it

APHIS--the Animal and Plant Health Inspection Service, part of the U.S. Department of Agriculture

astroturf--pads of short, artificial grass

AWA--Animal Welfare Act (7 U.S.C. 2131 et. seq.) Section 13. (a) (2) (B) pertains to the promulgation of standards to govern the humane handling, care, treatment and transportation of animals by dealers, research facilities, and exhibitors. The standards shall include minimum requirements for exercise of dogs.. and "for a physical environment adequate to promote the psychological well-being of primates."

AWIC--the Animal Welfare Information Center, part of the U.S. Department of Agriculture

Berlin Workshop--*the International Workshop on the Accommodation of Laboratory Animals in Accordance with Animal Welfare Requirements, Berlin 17-19 May 1993*

brachiate--to progress by swinging while suspended from one hold to another by the hands

CCAC--Canadian Council on Animal Care

conspecific--individuals of the same species

Email--electronic messaging through computer networks

gustatory--pertaining to the sense of taste

intraspecific--occurring within a species or involving members of one species

isosexual--a pair or group of animals all of the same sex

manipulanda--things to move, treat, or operate with the hands

minimalistic--using the fewest and simplest elements

monogamous--having only one mate at a time

NHP--nonhuman primate

NIH--the National Institutes of Health, part of the U. S. Department of Health and Human Services

neophobia--fear of anything new

nocturnal--active at night

nonresponsive--not giving an action in return when touched or moved

NRC/ILAR--the National Research Council, Institute for Laboratory Animal Research

olfactory--pertaining to the sense of smell

phylogenetically remote--species that are genetically very distant and unlike

polyandrous--having more than one male mate at a time

polygamous--having more than one mate at a time

preformulated--mixed together according to a formula in a factory before sale

primatological--pertaining to the study of primates (apes, monkeys and related forms)

PWB--psychological well-being

reingestion--taking in for digestion a second time

resocialize--to readjust to a social group or partner after an absence

sociality--social nature

stereotypy--frequent, mechanical repetition of the same posture or movement

sternally--on the chest or front side

surrogate--a substitute

thermoconductive--transmitting heat or cold through it

webpage--a page of information displayed on the World Wide Web computer network

xenophobia--fear of strangers or foreigners or of anything that is strange or foreign

APPENDIX C. Sample Species Information Sheets

In order to help APHIS inspectors and facilities understand better how to enhance the psychological well-being of nonhuman primates they inspect or own, APHIS is attemping to develop some resource materials for distribution. Sheets like the following will be drafted for the primates species found most commonly in the U.S. At this point in time, they are only illustrative of the final product, and will be changed when we have experience drafting several more. They give some useful facts about the primate species, how they live in the wild, suggest options or strategies for meeting the critical elements, and list sources for further research. The details are recommendations, not absolute requirements. We hope they provide an idea of the acceptable range of variation for facilities' plans.

The page numbers of this appendix are not in sequence--only the sample pages are included.

APPENDIX C:

Species Information Sheets - Table of Contents - 2/8/99

Name: *Ateles geoffroyi panamensis* (Central American spider monkey)

Morphology: The spider monkey's tail is well adapted for seizing or grasping and is called prehensile. The sole or bottom skin surface is hairless and has grooves like fingerprints that enhance its ability to grasp branches. Spider monkeys use their tails as fifth limbs and can support the whole weight of their bodies with them. They have flexible shoulder joints for swinging from one branch to another (brachiating). Their arms are elongated and their hands are adapted into suspensory hooks. Thumbs are absent or very small, and the fingers are long and permanently curved. *A. geoffroyi* lives in Central America and is also known as the black-handed spider monkey and is distinguished by having hair that is light in color (buff or reddish). Its neighbors in South America (*A. fusciceps*, *A. paniscus*, and *A. chamek*) tend to be black.

Postures: Spider monkeys sit, lie in all positions, and stand erect with arms stretched vertically. They feed while suspended from their tails in tree branches and use their tails as anchors. Their suspensory postures are probably an adaptation that allows them to reach food at the end of thin branches.

Locomotion and positions: Spider monkeys walk well on two legs, bipedally. They also walk, run, and leap on four legs, quadrupedally, with their bodies held horizontally. They brachiate frequently and superbly, almost as well as gibbons. In bridging from one tree to another, the spider monkey commonly grasps the base tripedally with hind feet and tail and reaches for the target with its hands. Spider monkeys tend to keep their heads upward and descend feet first. They frequently make long jumps outward and downward, covering great distances.

Habitat: Spider monkeys have been found throughout Central America from Veracruz, Mexico to Panama. They inhabit old, tall, spacious forests of evergreens, semideciduous trees, and mangrove trees. They adapt readily to changes in climate and do not sleep in holes in trees. While early accounts suggest that they were contemptuous of potential predators at one time, in modern times they are being hunted for food and have become shy of man. They are listed as vulnerable by the World Conservation Union and their survival is threatened by the increasing destruction of the forest by humans.

Feeding, food, diet: The *geoffroyi's* diet consists of more than three quarters fruit--high quality, energy-rich fruit, which is hard to find and widely scattered. They travel long distances in big home ranges to maximize their fruit intake. Small fruits are swallowed whole without chewing and the

seeds dispersed. The remainder of their diet consists of decreasing percentages of seeds, flowers, young leaves, buds, mature leaves, and animal prey. (The animal prey could be insects, larva, bird eggs, and baby birds.)

Sensory uses, adaptations: *Tactile*: Lacking thumbs, spider monkeys are not good manipulators. However, the naked skin on their tails contains sweat glands and sensory nerve endings similar to those on hands. Females pick through the hair of their young, making long downward currying movements, parting the hair and searching over the skin, but do not frequently explore the hair and remove particles as do macaques and capuchins. *Olfactory:* Spider monkeys have glands near the base of the neck that appear to give off olfactory signals. Their stereotyped embrace and pectoral sniffing behavior are probably olfactory examinations of these glands. Rubbing their chests with their hands or arms and then against objects may transmit the secretions for scent marking purposes. Males like the smell of the urine of females. *Auditory*: Their auditory sense is well developed and used for vocal communication.

Communication: Spider monkeys communicate vocally to keep in touch with each other while eating and traveling. Their repertoire of sounds includes: a terrier-like bark signaling the approach of strangers; growls given by adults when closely approached by strangers or when contending subgroups are aroused; and high-pitched whinnies given when subgroups or individuals become separated and need to be coordinated with the others. Captive infant spider monkeys do not utter play vocalizations. Postures and bodily attitudes are means of communication that are taught to infants by their mothers. Some facial expressions have become associated with certain states of motivation and call forth responses. The protruding lips, squinted eyes and wrinkled forehead seem to indicate an attitude of approach and friendliness. The half-open mouth emitting a series of grunts seems to indicate sexual receptivity. In aggressive situations such as response to human intruders, spider monkeys put on vigorous branch shaking displays, accompanied by scratching and staring.

Social Structure, social behavior, reproduction: Black-handed spider monkeys congregate in large troops, up to 35, when resources permit. These may consist of one or more females with one or more young, one or more males with many females, or a group comprised of all males. Groups having a large number of individuals in the early morning may disband by midmorning and regroup with different individuals in the afternoon.

Groups of spider monkeys seem to have no highly centralized social control. Social control is diffuse. The few instances of fighting that he observed consisted of males contending with each other. Male aggressive behavior is infrequent and directed towards other males when it occurs, and adult males are ranked in a dominance order. Male spider monkeys spend less time feeding at each site and travel farther than females. Males have the largest territories. There are also dominance relations among some females. Spider monkeys occasionally associate with white-throated capuchins (*Cebus capucinus.)*

A great variety of play patterns is shown by young spider monkeys, but little play occurs among adults. Play consists of running, jumping from one branch to another, standing still and jumping up and down, swinging from a limb, and playing with sticks or other objects. Young spider monkeys may chase each other for hours over circuitous routes, or may catch and bite each other. Wrestling occurs when they are sitting on limbs or swinging by their tails.

Development, parental care: *Infancy*: 0 - 24 months. During the first six months of their lives, young spider monkeys are almost entirely dependent on their mothers. This dependency continues until they are well into their reddish color phase, about ten months of age. Infancy is from 0 to 24 months (Milton 1973), the longest known period of dependency of any cebid. Infants ride on their mothers' backs. The mother may control the movements and postures of her infant by forceful directing. Thereby the behavior of the two animals becomes coordinated. After repetition, the young come to respond to reduced cues and postures and bodily attitudes become means of communication. *Sexual maturity*: 48 - 60 months. The estrus cycle is 26 days. *Gestation*: 226 - 232 days. *Birth intervals*: 17 - 45 months. *Life span*: 27 years.

Other special behaviors, adaptations: Spider monkeys spend over half their time resting, a quarter traveling, and about 10 percent feeding. There is no sexual dimorphism in body size. The clitoris of the female is long and pendulous and females can be misidentified as males.

Enrichment Strategies Recommended:

1. Social Grouping: It is recommended that spider monkeys be housed in groups composed of a single male with multiple females. A troop with several adult males and females and a variety of young of different ages is desirable if the members are compatible.

2. Social Needs of Infants: Infant spider monkeys should stay with their mothers at least 6 months. If possible they should be allowed to stay until they stop nursing, which may be much longer.

3. Structure and Substrate:

Cage structure must allow for species-typical resting and brachiation. Ropes, swings, multiple level perches and branches for climbing, jumping, and swinging.

Adequate vertical space and postural supports to enable all animals to move and perch with their tail hanging in a normal position of rest without

touching the floor.

Space for jumping, laterally and vertically, and brachiation.

It is also important to have boxes or hiding areas which offer visual barriers.

4. Foraging Opportunities:

Task oriented feeding such as: offering food on the outside of the enclosure and requiring the animals to get it through the bars or wire; hanging food and requiring them to eat while suspended; and hiding fruit or popcorn in mesh or paper bags filled with straw or shredded paper.

Browse placed in natural positions, upright or hanging down.

If the floor is solid, seeds, fruit, and nuts scattered in litter composed of straw, leaves, wood shavings, or corn cobs.

Puzzle feeders or pipe feeders

5. Manipulanda:

Test various simple objects to see if they can be manipulated with hands, feet, and tails.

Try items that provide stimulation of other senses, such as balls, chew toys, and rattles.

6. Sensory Stimulation:

Mirrors that can be used to view the outdoors, care givers, other primates, or around the room.

Taped sounds of their species, radios, TV

Scent-marking articles (logs, sticks, rags, or plant material)

Sanitation procedures should take into consideration the possible importance of odors for the cage inhabitants. The presence of odors should not be taken to mean that sanitation is inadequate.

Varied food texture, smell, and flavor (hot, sour, or pungent.)

Naturalistic settings (branches, tree limbs, vines, and floor litter).

7. Novelty and Control: Spider monkeys cannot explore or control some features of their surroundings as intensively or efficiently as monkeys which have hands that can do more things. However, they have large and complex brains, appear to be very intelligent, and are the most adaptable of *ceboids* in locomotory patterns and some of their social reactions. Given this, it seems that periodic changes in ropes, swings, perches, and branches would be especially appropriate.

Note: The National Research Council (1998:66-74) gives information on proper housing temperatures, nutrition, personnel procedures, veterinary care, and other topics.

RESOURCES

General Sources with Material on This Species

Bramblett, Claud A. (1976). *Patterns of Primate Behavior.* Mayfield Publishing Company: Palo Alto, California. NAL Call Number QL737.P9B747

Kleiman, Devra G., Mary E. Allen, Katerina V. Thompson, and Susan Lumpkin (1996). *Wild Mammals in Captivity.* Harris, Holly, (Managing editor). The University of Chicago Press: Chicago, Illinois, pp. 67 - 77.

MacDonald, David (1995). *The Encyclopedia of Mammals.* Facts n File Inc.: New York, pp. 358 - 369.

Moynihan, Martin (1976). *The New World Primates: Adaptive Radiation and the Evolution of Social Behavior, Languages, and Intelligence.* Princeton University Press: Princeton, New Jersey.

National Research Council, Institute for Laboratory Animal Research, Committee on Well-Being of Nonhuman Primates (1998). New World monkeys: *Cebids*. In *The Psychological Well-Being of Nonhuman Primates.* National Academy Press: Washington, D.C., pp. 66-74.

Rowe, Noel (1996). *The Pictorial Guide to the Living Primates*. Pagonias Press, East Hampton, New York, pp. 113-115.

Smuts, Barbara B., Dorothy L. Cheney, Robert M. Seyfarth, Richard W. Wrangham, and Thomas T. Struhsaker, eds. (1987). *Primate Societies*. University of Chicago Press: Chicago, Illinois, 578 pp. NAL Call Number: QL737 P9P67

Wolfheim, Jaclyn H. (1983). *Primates of the World: Distribution, Abundance, and Conservation*. University of Washington Press: Seattle, Washington. NAL Call Number QL737.P9W64.

Sources on this Species

Blakeslee, B. and G. H. Jacobs (1982). Color vision in the spider monkey (*Ateles*). *Folia Primatologica* 38(1-2):86-98.

Cant, J. G. H. (1978). Population survey of the spider monkey (*Ateles geoffroyi)* at Tikal, Guatemala. *Primates* 19(3):525-535.

Carpenter, C. R. (1935). Behavior of red spider monkeys in Panama. *Journal of Mammalogy* 16:171-180. NAL Call Number 410 J823

Chapman, C. A. (1989). Spider monkey sleeping sites: use and availability. *American Journal of Primatology* 18(1):53-60.

Chapman, C. A., and L. J. Chapman (1987). Social responses to a traumatic injury of a juvenile spider monkey (*Ateles geoffroyi)*. *Primates* 28(2):271-275.

Chapman, C. A., Chapman, L. J., and L. Lefebvre (1990). Spider monkey alarm calls: honest advertisement or warning kin? *Animal Behavior* 39(1):197-198.

Chapman, C. A. and L. Lefebvre (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behavior* 39(5):891-896.

Chapman, C. A., Wrangham, R. W. and L. J. Chapman (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36(1):59-70. January, 1995.

Eisenberg, J. F. (1983). *Ateles geoffroyi (mono arana, mono colorado)*, spider monkey. In *Costa Rican natural history*. Janzen, D. H., ed. University of Chicago Press: Chicago, Illinois, pp. 451-453.

Estrada, A., (1082). A case of adoption of a howler monkey infant *Allouatta villosa)* by a female spider monkey *(Ateles geoffroyi*). *Primates* 21(1):135-137.

Izawa, K., Kimuro, K., and A. S. Nieto (1979). Grouping of the wild spider monkey. *Primates* 20(4):503-512.

Julliot, C. (1994). Predation of a young spider monkey (*Ateles paniscus)* by a crested eagle *(Morphnus guianensis)*. *Folia Primatologica* 63(2):75-77. December, 1994.

Kinzey, Warren G., ed. (1997). Chapter 13: Ateles. In *New World Primates: Ecology, Evolution, and Behavior.* Aldine De Gruyter: New York, 192-199. NAL Call Number QL 737 P925N48

Klein, Lewis L. and Dorothy J. Klein (1971). Aspects of social behavior in a colony of spider monkeys (*Ateles geoffroyi*) at San Francisco Zoo. *International Zoo Yearbook* 11:175-81.

Klein, Lewis L. and Dorothy J. Klein (1975). Social and ecological contrasts between four taxa of Neotropical primates. In *Socioecology and psychology of primates,* Tuttle, R., ed. The Hague, Mouton: Chicago.

Laska, M, Carrera-Sanchez, E., Rodrigues-Rivera, J. A., Rodrigues, and E. Luna (1996). Gustatory thresholds for food-associated sugars in the spider monkey (*Ateles geoffroyi)*. *American Journal of Primatology* 39(3):189-193.

McDaniel, P. S., Janzow, F. T., Porton, I., and C. S. Asa (1993). The reproductive and social dynamics of captive *Ateles geoffroyi* (black-handed spider monkey). *American Zoologist 33(2):173-179.*

Milton, K. (1993). Diet and social organization of a free-ranging spider monkey population: the development of species-typical behavior in the

absence of adults. In *Juvenile primates: life history, development, and behavior*. Pereira, M. E. and L. A. Fairbanks, eds. Oxford University Press: New York and Oxford, pp. 173-181.

Pingry, K. (1997). Studbook for the Central American spider monkey, *Ateles geoffroyi.* In *Neotropical Primates* 5(1):13. March, 1997.

Sodaro, V. (1993). Hand-rearing and reintroduction of a black-handed spider monkey *Ateles geoffroyi* at Brookfield Zoo, Chicago. *International Zoo Yearbook* 32:224-228.

Stegenga, L. (1993). Modifying spider monkey behavior with the use of environmental variables. *Shape of Enrichment* 2(3):3-4. August, 1993.

GLOSSARY

Arboreal: Adapted to life in the trees

Bipedal: Using only two limbs for locomotion, as in humans or birds.

Brachiating: Swinging by the hands from one branch to another.

Dimorphism: (Sexual) Size, color, or weight variation between genders of the same species

Manipulanda: Items/objects that can be handled/manipulated

Olfactory: Related to the sense of smell

Quadrupedal: Using four limbs for locomotion

Sole: (of the tail) The bottom (ventral) skin surface

Name: *Cebus apella* (tufted, black capped or brown capuchin monkey)

Morphology: Medium sized monkey with head and body length equal to the tail length. Bodies are robust and heads are rounded. Limbs are rather short, especially the arms. Tail is semi-prehensile and is lacking a prehensile sole. Has a thick mat of erect brown hairs on the crown, sometimes forming tufts at the side of the head. The brain is extremely large in relation to body weight.

Postures and locomotion: Basically quadrupedal (86%) with leaping (7%) and climbing (6.5%). Jumps up to 10-12 feet. The tail adds postural support. Rests in a sitting position or curled up on its side or stretched out on a branch with arms and legs dangling, but always with tail tip anchored to a branch.

Habitat: *C. apella* is the most widespread of the capuchin species. Has the largest range of any New World monkey. Found throughout South America east of the Andes in subtropical and tropical forest, except Uruguay and Chile. Prefers moister forests than other capuchins and ranges to higher elevations. Normally occupies under story trees 5 to 20 meters high with crowns less than 10 meters in diameter.

Feeding, food, diet: Capuchins are frugivore-insectivores whose diet includes both fruits and invertebrates. *C. apella* is particularly fond of cumare and palmnut. It uses special nut cracking techniques to reach the kernel. It is also adept at catching and eating tree frogs which it extracts from bamboo trunk cavities. It is very adaptable and may exploit over 90 plant species a year. It eats more vegetation and larger fruits than other species. Bark stripping and breaking open branches to hunt for insects. Overall body size and strong jaws allow proficient manipulation of tough foods.

Sensory uses: *Olfactory:* Scent marker with each individual maintaining olfactory identity by washing palms and feet with its urine (urine washing). Rub plants and other items in their environment into their fur. *Tactile:* Tactile sense is well developed with excellent manipulative ability. Highly intelligent species of neotropic primates. Typically pick up, handle, visually inspect, bite, pull, hit and rub any nonthreatening objects encountered.

Communication: Vocalizations including a variety of chatters, squeaks, shrieks, and other sounds for communication, facial expressions, lip smacking and urine washing. Chemical signals might identify an individual animal's sex and play important roles in reproductive behavior, aggressive interactions, and other kinds of behaviors.

Social structure, behavior, reproduction: Diurnal and arboreal. Socialize in multimale-multifemale groups, usually with an equal number of males and females. Group size is usually 3-15 with one dominant male and one dominant female. Groups composed of 1-4 adult and subadult males, 1-4 adult and subadult females, and their juvenile offspring. Dominant males serve as watchdogs and protectors of social groups. Adult males form affiliations and there is a high degree of tolerance among males within social groups. Play fighting is the primary form of social contact

among males, among juveniles, and between males and juveniles Adult females interact with adult females and juveniles. Social contact between females consists primarily of mutual grooming and sitting in close contact. Male emigration to other troops occurs between 3-5 years of age. Males are sexually mature at 5 years of age and females around 4 years. Adult and subadult females are more likely than males to engage in aggressive behavior. Kin-relations are important in establishing stable groupings.

Infant development and parental care: During the first month of life the infant is carried transversely on the back of its mother, then longitudinally thereafter. Mothers and siblings frequently interact with infants during the first 6 months of life and it is termed the 'kin phase'. Aside from the mother, siblings are the most important social partners during the 'kin phase'. Allomothering is common. Infants can be carried by adults and juveniles other than the mother. The second 6 months are termed the 'peer phase' for infants because of frequent interaction by the infant with other infants and juveniles one year older. Infants still maintain close contact to kin-related animals during the 'peer phase'. Grooming of infants is primarily done by the mother and older female siblings. Age of weaning is 12 months.

Other special behaviors, adaptions: Adept with their hands and exhibit precision grips that require independent control of digits. Tool using has been reported. Persistent manipulators of objects. Show extreme interest in the manipulative activities of other capuchins. Utilize special nut cracking techniques and are noted for their ingenuity in extracting tree frogs from cavities in bamboo trunks. Urine washing as a marking behavior is thought to be used only in Cebus species.

The National Research Council (1998:72) reports that, "Capuchins.. show greater manipulative ability than rhesus monkeys and are the prototype of the active monkey for which provision of opportunities for productive activity is essential to well-being. When not locomoting, they are most often busy with their hands.. When no other opportunities are present, their attention is directed to surfaces in the cage or nearby objects, such as locks. This activity can be safely redirected by providing them with such objects and materials as wood, soft plastic, straw, and small containers.. They will spend much time shredding and destroying disposable objects. They also retain interet in objects that require dexterous probing or scraping."

Enrichment Strategies Recommended

1. Social Grouping:

It is recommended that capuchins be housed in single male and multiple female groups. When sufficient space is available, provide interior walls or hanging panels to allow segregation and sanctuary and establish multiple male/multiple female groups.

Kin-relations are important to establishing multiple male/multiple female groups.

2. Social Needs of Infants: Infants should not be removed from their mother/sibling unit until at least 1 year of age.

3. Structure and Substrate:

Solid floored cage with bedding material of straw (preferably) or other materials that provide manipulative opportunities.

Tire swings, suspended perches suitable for resting, climbing ropes, natural branch structures which allow tail grasping.

Hanging rubber panels and interior walls for natural group segregation.

Adequate vertical space and postural supports to enable all animals to move and perch with their tail hanging in a normal position of rest without touching the floor.

Space for jumping laterally and vertically.

4. Foraging:

Scatter seeds, diced vegetables, hard shell nuts and other relished treats in the bedding.

Provide puzzle feeders that require persistent manipulation to acquire food items.

Provide complex foraging units with visual and hidden cavities for touch dependent foraging

Nut boards

External food or liquid wells that require tool use (sticks, straw etc.) to acquire foods

Pipe feeders

Mechanical or electrical food dispensers

Suspended or cage top feeding

5. Manipulanda:

Novel objects of wood or soft plastic; containers

Portable objects (such as sticks or straw) that can be used as probes or tools

Indestructible toys, especially those with moving parts

Problem box tasks that stimulate cognitive behaviors

Branches with attached bark or disposible objects to shred or destroy.

6. Sensory Stimulation:

Naturalistic settings/substrates

Group housing

Wide variety of fruits, nuts, vegetables, and invertebrates that provide olfactory, gustatory and textural stimulation.

Wide variety of toys with different textures and both visual and manipulative complexities.

Sanitation procedures should take into consideration the possible importance of odors for the cage inhabitants. The presence of odors should not be taken to mean that sanitation is inadequate.

7. Novelty and Control:

Rotate different types of bedding substrate

Provide novel and seasonal food items/treats/foliage

Vary treats/food items within foraging tasks

Vary types of toys and manipulanda

Periodically rotate in and rearrange perches and climbing structures

Note: The National Research Council (1998:66-74) gives information on proper housing temperatures, nutrition, personnel procedures, veterinary care, and other topics.

REFERENCES:

Anderson, J. R., Combette, C., and Roeder, J. J. (1991). Integration of a tame adult female capuchin monkey (*Cebus apella*) into a captive group. *Primate Report* 31:87-94.

Fragaszy, D. M. and Adams-Curtis, L. E. (1991). Environmental challenges in groups of capuchins. In H. O. Box (Ed.), *Primate Responses to Environmental Change* (pp.237-264). New York: Chapman and Hall.

Hayes, S.L. (1990). Increased foraging opportunities for a group of captive capuchin monkeys (*Cebus capucinus*). *Laboratory Animal Science* 40[5],(pp.516-519).

Janson, C. H. (1984). Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). *Zeitshrift fuer Tierpsychologie* 65(3):177-200.

Janson, C. H. (1998). Capuchin counterpoint. In *The Primate Anthology: Essays on Primate Behavior, Ecology, and Conservation from Natural History*, Ciochon, Russell L. and Nisbett, Richard A., eds. Prentice Hall: Upper Saddle River, New Jersey, pp. 153--160. Reprinted with permission

from *Natural History* (February, 1986), American Museum of Natural History.

Kinzey, W. G. (Ed.) 1997. *New World Primates: Ecology, Evolution, and Behavior*, (pp. 248-57), New York: Aldine de Gruyter (A division of Walter de Gruyter, Inc.).

Ludes, E. and Anderson, J. R. (1995). Introduction of an unfamiliar female capuchin monkey *(Cebus apella)* into a group in captivity. *Mammalia* 59(3):307-313.

McDonald, D. (Ed.) 1995. *The Encyclopedia of Mammals, (*pg. 360), New York: Facts On File, Inc.

Munkenbeck-Fragaszy, D. (1989). Activity states and motor activity in an infant capuchin monkey *(Cebus apella)* from birth through eleven weeks. *Developmental Psychobiology* 22(2):141-157.

National Research Council, Institute for Laboratory Animal Research, Committee on Well-Being of Nonhuman Primates (1998). New World monkeys: *Cebids*. In *The Psychological Well-Being of Nonhuman Primates.* National Academy Press: Washington, D.C., pp. 66-74.

Napier, J. R. and Napier, P. H. (1985). *The Natural History of the Primates, (*pg.114), Cambridge, Massachusetts: The MIT Press.

Nowak, R. M. and Paradiso, J. L. (1983). *Walker's Mammals of the World,* 4, (pg.402), Baltimore: The John Hopkins University Press.

Phillips, K. A. (1993). Mating patterns and sexual competition in Brown capuchin monkeys(*Cebus apella)*: Implications for captive housing. AAZPA 1993 Regional Proceedings.

Ritchie, B. G. and Fragaszy, D. M. (1988). Capuchin monkey (*Cebus apella*) grooms in infant's wound with tools. *American Journal of Primatology* 16(4):345-348.

Robinson, J. G. and Janson, C. H. (1987). Capuchins, squirrel monkeys, and atelines: Socioecological convergence with Old World primates. In D. L. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker (Eds.), *Primate Societies,* (pp.69-82), Chicago: The University of Chicago Press.

Rowe, Noel (1996). *The Pictorial Guide to the Living Primates,* (pp.93-97), East Hampton, New York: Pogonias Press.

Ueno, Y. (1994). Olfactory discrimination of eight food flavors in the capuchin monkey (*Cebus apella)*: comparison between fruity and fishy odors. *Primates* 35(3):301-310.

Weigel, R. M. (1979). The facial expressions of the brown capuchin monkey (*Cebus apella). Behavior* 68(3-4):250-276.

Welker, C. (1992). Long-term studies on the social behavior of the capuchin monkey *(Cebus apella)*. In *Perspectives in primate biology. Vol. 4: Primates--the new revolution.* Seth, P. K. and S. Seth, eds. Today and Tomorrows Printers and Publishers: New Delhi. pp. 9-16.

Welker, C., Becker, P., Hohmann, H., and Schafer-Witt, C. (1987). Social relations in groups of Black-capped capuchin(*Cebus apella)* in captivity: Interactions of group-born infants during their first 6 months of life. *Folia Primatol* 49, (pp.33-47).

Welker, C., Becker, P., Hohmann, H., and Schafer-Witt, C. (1990). Social relations in groups of Black-capped capuchin (*Cebus apella)* in captivity. *Folia Primatol* 54, (pp.16-33).

Welker, C., Hohmann-Kroger, H., and Doyle, G. A. (1992). Social relations in groups of Black-capped capuchin monkeys,(*Cebus apella)* in captivity: mother-juvenile relations from the second to the fifth year of life. *Z. Saugetierkunde* 57, (pp.70-76).

Welker, C. and Hohmann-Kroger, H. (1989). To the social structure of the Black-capped capuchin (*Cebus apella cay)* Illinger,1815. Results of a long-term study on stable social groups in the laboratory. *Medio Ambiente,* 10[2], (pp. 129-35).

GLOSSARY

Allomothering: Care of an infant by a group member other than its mother; (similar to babysitting)

Arboreal: Adapted to life in the trees

Diurnal: Active during the day

Frugivore: An animal that eats fruit as a major percentage of its diet

Gustatory: Of tasting, or the sense of taste

Insectivore: An animal that eats insects as a major percentage of its diet

Manipulanda: Items/objects that can be handled/manipulated

Neotropic: The tropical regions of Central and South America

Olfactory: Of smelling, or the sense of smell

Prehensile: Able to grasp while wrapping around. Often refers to tails of some larger Neotropic monkeys

Quadrupedal: Using four limbs for locomotion

Sole (of the tail): The bottom (ventral) skin surface

1. A standard is called "performance-based" because it relies on qualities of the result or end-product of facility activity and allows facilities to decide how best to achieve results. They must document their decisions in "performance plans." When a standard is performance-based, facilities are responsible for the results and are encouraged to constantly examine and improve their methods. This kind of a standard contrasts with so-called "engineering" or "design" standards which specify exact methods. Design standards are presumed to allow less latitude for the facility than performance-based standards. Performance-based standards may be difficult to use and enforce if their end-points are not well-defined. The Institute for Laboratory Animal Resources' (ILAR's) *Guide for the Care and Use of Laboratory Animals* states, "Optimally, engineering and performance standards are balanced, thereby providing standards while allowing flexibility and judgment based on individual situations" (NRC/ILAR 1996:3).

2. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Animal Care (1996). USDA Employee Opinions on the Effectiveness of Performance-Based Standards for Animal Care Facilities. USDA, APHIS: Riverdale, Maryland, December, 1996. The study also evaluated 9 CFR, Part 3, Subpart A, 3.8, Exercise for Dogs.

3. However, at research facilities animals may be housed or used in exception to any standard if the alternative treatment is scientifically justified and documented in an experimental protocol approved by an Institutional Animal Care and Use Committee.

4. Kessel and Brent 1995a and 1995b (baboons), Salzen 1989 (squirrel monkeys), Seier and de Lange 1996 (vervets), Tustin *et. al.* 1996 (Japanese macaques), Brent *et. al.* 1991 (chimps), Eichberg *et. al.* 1991 (chimps), Bennett and Davis 1989 (rhesus monkeys), Blackmore 1989 (macaques), Gilbert and Wrenshall 1989 (long-tailed macaques), King and Norwood 1989 (squirrel monkeys), Lynch and Baker 1998 (long-tailed macaques), Taylor and Laudenslager 1998 (pig-tailed macaques), Wolff and Ruppert 1991 (rhesus and cynomologous macaques and capuchins), Chance *et. al.* 1983 (cynomologous macaques).

5. Weed *et. al.* 1995 (baboons), Doyle *et. al.* 1996 (baboons), Kaplan and Lobao 1991 (rhesus), Adams and Britz 1997 (baboons), Burt and Plant 1990 (stump-tailed macaques), Applebee *et. al.* 1991 (rhesus)

6. Brent *et. al.* 1991, Kessel and Brent 1995a and 1995b, Taylor and Laudenslager 1998, Schoenfeld 1989, Perkins 1992, Seier and deLange 1996, Marriott *et. al.* 1993, Tustin *et. al.* 1996, Kerl and Rothe 1996, Clarke *et. al.* 1982, Wolff and Ruppert 1991, Blackmore 1989, Bryant *et. al.* 1988, Tolan *et. al.* 1980, Fouts *et. al.* 1989, Leu *et. al.* 1993.