BEHAVIORAL EFFECTS OF EXPOSING CAPTIVE COTTON-TOP TAMARINS TO CONTROLLED AUDITORY STIMULI

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in
Biology: Physiology and Behavior

by

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CERTIFICATION OF APPROVAL

I certify that I have read *Behavioral Effects of Exposing Captive Cotton-Top Tamarins to Controlled Auditory Stimuli* by Chris Thomas Tromborg, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirements for thedegree: Master of Art in Biology: Physiology and Behavior at San Francisco State University.

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This study explores changes in several species-specific behaviors that occur during the presentation of eight ecologically relevant auditory stimuli to a pair of vocally active primates, cotton-top tamarins (*Saguinus oedipus oedipus*), housed in a contemporary zoo setting. The two captive cotton-top tamarins were exposed to acoustic conditions which included the vocalizations of captive conspecifics, those of free-living Geoffroy's tamarins, and the stridulations of cicadas, a common prey item. When the treatments were administered to the subjects in a fixed sequence at 20-minute intervals over a period of nine months, the animals showed a significant increase in autogrooming ($p < .01$) and total vocalizations ($p < .001$), while simultaneously showing a significant decrease in allogrooming ($p < .001$) and scanning ($p < .001$) compared to previously obtained baseline measures. Foraging/environmental exploration, display, scent marking, and sexual behavior showed no significant differences when the baseline totals were compared to those for the treatment conditions. These results suggest that increasing the acoustic complexity and naturalness of captive habitats offers a practical means for modulating the behavior of captive primates, i.e., increasing desirable behaviors while possibly diminishing abnormal behaviors.

I certify that the Abstract is a correct representation of the content of this thesis.

______________________________________ __________

(Chair, Thesis Committee) (Date)

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Behavioral Effects of Exposing Captive Cotton-top Tamarins to Controlled Auditory Stimuli

The increasing rate of decline of many species in the wild and the growing importance of endangered species in conservation education and research require that improved techniques of animal husbandry be developed. Conservation biology and education of the public to the plight of the flora and fauna of the planet are becoming increasingly important functions of progressive zoological gardens. This study addresses questions relating to the efficacy of environmental enrichment through behavioral engineering for captive animals; the usefulness of behavioral research utilizing zoological gardens as the location for biological research; and, finally, the applicability of the findings presented to the improvement of conditions found in other institutions housing captive animals. This study explores the concept of increasing the acoustic complexity of the surroundings of captive primates housed in an acoustically unnatural habitat as a means of improving the sensory richness of their surroundings.

Studies of animals in captivity have become increasingly important in recent years as a result of changing philosophies of captive animal management, especially on the part of zoological gardens. Historically, the primary role of zoological parks was one that emphasized recreation and entertainment for their visitors (Hediger, 1964/1950). Supervisors of institutions housing animals for the purposes of research or entertainment perceived the supply of wild animals as inexhaustible. Little emphasis was placed on the long-term management of captive wild animal populations. Specimens that did not survive well in captivity were easily replaced with new animals recruited from the wild. Few attempts were made to determine causal factors resulting in the high rates of mortality prevailing in many captive animal populations (Carpenter, 1983; Conway, 1974).

The increasing human population, with its concomitant demands on decreasing natural resources and the simultaneous explosion in the use of certain animals in biomedical research, has placed severe pressure on wild populations of formerly abundant species. These conflicting trends are especially evident in the case of some neotropical primates, many of which are commonly found in zoo collections and have become important to the biomedical research community. Poor survivability in captivity necessitates research that results in decreased mortality and improved fecundity. In this way, future recruitment of replacement individuals will come from established captive colonies and not from declining natural populations (Lindburg, Berkson, & Nightenhelser, 1986).

While zoos can never replace nature, zoo habitats can be improved in ways that emulate aspects of an animal's habitat and offer animals greater opportunities to exercise species-typical behaviors (Markowitz, 1975). There is a critical need to determine which components of captive habitats can be manipulated to provide greater opportunities for the expression of natural behaviors (Markowitz & Spinelli, 1986). An appropriate species for studying the influence of captivity on behavior and observing the results of environmental improvements would be one that is endangered, has proven to be difficult to maintain in captivity, is known to respond to changes in its surroundings, and is available at an institution with representative facilities.

The cotton-top tamarin (*Saguinus oedipus oedipus*) is one such species. When combined with a complex habitat, relatively acoustically isolated from extraneous zoo sounds, a situation arises which offers an opportunity to test a particular behavioral enrichment model: the improvement of artificial habitats through the application of ecologically relevant sounds. Cotton-top tamarins are diminutive New World primates which are disappearing in the wild and have proven to be difficult to maintain and breed in captivity. Increased breeding success in zoos and laboratories is necessary, partly because of their desirability as zoo specimens and their growing importance in biomedical research (Gay, 1986). The discovery of environmental variables which, when manipulated, seem to improve breeding success and survival, or at least reduce locomotor stereotypies, might assist institutions attempting to manage captive populations of these animals.

Another broad area of concern is the influence exerted on captive animal populations over generations. Wild animals that have been brought into captivity are adequately housed, immunized against disease, and protected from extreme environmental conditions, including predation (Hediger, 1964/1950). It is probable that animals which have been in captivity for several generations display genotypic and phenotypic differences when compared to their wild counterparts. This is an important consideration if managers of captive animal populations entertain plans for the reintroduction of captive animals to areas from which they have been extirpated.

Captive habitats should be as similar as possible to those in which a species has evolved. Naturalistic re-creations of wildlife habitats can improve the public's perception of captive endangered species, especially if aberrant behavior is reduced as a result of habitat improvements (Sommer, 1972). However, simply creating habitats which appear natural and pleasing to the zoo visitor through the planting of vegetation and the introduction of natural-appearing substrates in an attempt to re-create nature is not sufficient (Markowitz, 1982). Artificial habitats must feature ecological relevance for captive animals; the quality, as well as the quantity of, space must be considered (Maple & Finlay, 1986). Captive animals isolated from their ecological niches are often unable to perform meaningful behavior; they have, in a sense, lost their reasons for existing (Hediger, 1964/1950). Captive animals must be provided with habitats that allow them to express behaviors that, in nature, are necessary for survival.

While it is impractical to re-create the total environment of animals taken from the wild, certain elements of their former habitats can be replicated in captivity. Adequate habitats should feature naturalistic substrates; vertical complexity, especially for arboreal species; appropriate photoperiodicity, temperature, and humidity. These habitats should also allow opportunities for animals to engage in or escape from social interactions. Behavioral variability can also be encouraged by the use of more complex feeding regimens.

Some progressive zoos have attempted to replicate aspects of natural habitats in order to better instruct visitors about the natural history of their specimens. Fewer zoos have addressed the problem of educating the public about the behavior of captive wild animals. Zoos should begin to address this aspect of habitat design by providing interactive elements that enable animals to interact with their surroundings in meaningful ways (Markowitz, 1982). Occasionally, enclosures should be designed to allow the public to interact with some feature of the habitat. To the extent that zoo visitors are aroused by their zoo experiences, they will become more positively disposed toward zoos, animals, and the conservation of nature (Coe, 1985). To the greatest extent possible, the full behavioral and cognitive capabilities of all captive species should be accommodated, both for the benefit of the animals and to better educate the public (Markowitz & Spinelli, 1986).

Unfortunately, zoos must work within the limits of financial constraints, efficiency of maintenance, ease of observability, need for privacy for animals, and public concerns about animal welfare when exhibit design is being considered. These considerations usually result in the moderation of elaborate schemes for habitat improvement but do not necessarily eliminate the possibility for addressing the issues of behavioral enrichment. In some instances, interactive equipment can be installed in inadequate enclosures enabling animals to perform species-typical behaviors (Markowitz, Schmidt, & Moody, 1978; Markowitz, 1982). For example, environmental complexity can be augmented by increasing the richness of the acoustic habitat through the introduction of naturalistic sounds.

Cotton-top tamarins provide an opportunity to investigate the role of the acoustic habitat in affecting the behavior of a captive species. One aspect of the behavior of the cotton-top tamarin that has been well studied is its complex vocal repertoire (Cleveland & Snowdon, 1982; Epple, 1968). While research has addressed the function of specific elements of the vocal repertoire of these tamarins, there has been no prior attempt to use vocalizations to modify their behavior in captive settings. The incorporation of acoustic phenomena in a scheme designed to increase the sensory richness of a captive animal's habitat allows the following question to be posited: can the controlled exposure of captive cotton-top tamarins to the vocal signals of conspecifics and allopatric subspecies or other ecologically relevant sounds be employed to influence the locomotor, positional, and vocal behavior of captive cotton-top tamarins? This question generates the hypothesis that the rates of some behaviors will change under the influence of acoustic treatments. This hypothesis is tested in the following study by exposing a pair of cotton-top tamarins, located in a contemporary urban zoo, to ecologically relevant acoustic phenomena.

Environmental Enrichment

The Changing Role of the Zoological Garden

The paradigmatic shift in the fundamental mission of modern zoos from one emphasizing entertainment and conservation to one emphasizing education is correlated with a growing realization that animals might possess complex cognitive capabilities, can perform complex behaviors, and are increasingly imperiled in the wild (van Hooff, 1986). Historically, the zoological garden has emphasized the collecting and presentation of animals for the entertainment of the public (Hediger, 1964/1950). Due to limitations in transportation and communication, urban dwellers were seldom able to observe exotic fauna except at local zoos.

The development of the contemporary zoo began in earnest in the early 19th century with the construction of the Regent's Park Zoo in London (Brambell & Mathews, 1976). During the next 150 years, most large cities constructed zoological parks. The early emphasis was on the taxonomic diversity of specimens. Little consideration was given to the long-term management of animal populations. Animals that did not survive captivity could be easily replaced from abundant wild populations. Mortality rates for most species were high; not until the late 1960s was the relationship among housing, stress, and mortality firmly established (Snyder, 1975; Stoskopf, 1983).

In traditional zoos, animals sometimes manifested stereotypic and abnormal behaviors resulting from improper socialization and nonexisting behavioral opportunities (Meyer-Holzapfel, 1968; van Hooff, 1986). The unnatural housing and bizarre behaviors of captive animals did not effectively educate or promote respect for nature on the part of zoo visitors (Sommer, 1972). Animals were so uninteresting that the modal time visitors spent in front of a typical enclosure seldom exceeded ninety seconds (Brennan, 1977). The viewing of animals in concrete cages, behind steel bars, emphasized confinement and suggested that animals were little better than inmates in prison and certainly not as dignified as their wild conspecifics.

During the latter half of the twentieth century, the public awareness of growing environmental problems has brought about a desire for more relevant experiences in museums, zoos, and aquaria. There has been a confluence of the decline of wild animal populations with the changing role of the zoological garden (Conway, 1974). Progressive zoos are concerned with the long-term management of animal populations, attempting to preserve genetic diversity within limited gene pools, and are becoming producers rather than consumers of endangered animals (Holden, 1984; Lindburg, *et al.*, 1986). Individual animals are now seen as being valuable, and in some cases, irreplaceable. Animals that are displayed to the public are increasingly viewed as ambassadors of their species in informing the public about conservation issues (Western, 1986).

Increasingly, enclosures are designed to be not only attractive to zoo visitors but also more appropriate for the animals (Bertram, 1982). The presence of ecologically relevant features is now understood to be important for their welfare (van Rooijen, 1984). The concept of improving the habitats of captive animals in ways that increase their levels of activity as a way of assessing and improving their health status has also gained acceptance (Markowitz & Stevens, 1978).

While there continues to be criticism of zoos by those claiming that they are unnatural and inhumane, the concept of what constitutes a natural habitat is changing. As destruction of wilderness areas continues, the untouched regions of the planet shrink and become discontiguous. The wild is becoming increasingly artificial, more closely resembling some wild animal parks, or, in fact, the most naturalistic contemporary zoos, the best of which, in turn, attempt to replicate the wilderness (Hutchins, Hancocks, & Calip, 1978-1979). An important benefit of having zoo habitats resemble conditions under which a species has evolved is that animals held in captivity over many generations are less likely to diverge evolutionarily from the wild type (Eisenberg & Kleiman, 1977).

Among the many strategies for improving contemporary zoo habitats is the use of complex vegetation to impart apparent naturalism to enclosures. Increased horizontal and vertical complexity within an enclosure can dramatically increase the effective useable area within which an animal can move--often without expanding the physical dimensions of the enclosure (Thomas, 1986). There is a growing awareness that an increase in the physical size of an enclosure does not necessarily improve the habitat; its complexity must also be augmented (Erwin, 1986). Unfortunately, some enclosures that provide sufficient complexity and privacy also impede the viewing of animals by the public. Other changes in the physical structure of zoo exhibit designs include the replacement of traditional steel bars with glass, plexiglas, and "Perspex" walls. While these advances have ameliorated the prison-like appearance of many exhibits, the result is often reduction in buffer distance between the public and animals, possibly increasing stress in reactive species.

Although the trend toward larger, more complex habitats continues, not all zoological parks can afford these renovations. In some unfortunate cases, older, less appropriate enclosures can only be superficially modified. These modifications can include the introduction of interactive, manipulatable objects that provide animals in deficient enclosures with opportunities to perform certain types of behaviors, e.g., the opportunity to pursue automated prey (Markowitz, 1982). Addressing the issue of retrofitting older habitats is one of the compelling reasons for the development of the field of behavioral enrichment. The concept of behavioral enrichment through environmental engineering has gained acceptance by most captive animal managers. The primary goal of behavioral enrichment is to offer captive animals some degree of control over their surroundings. The ability of an animal to affect its habitat seems to result in fewer stereotypic behaviors and better long-term survivability (Greer, Diamond, & Murphy, 1982; Markowitz & Spinelli, 1986).

When animals behave less stereotypically they are more interesting to the public (Sommer, 1972). Further, to the extent that animals in captivity excite the public, visitors will remember a positive experience at the zoo and conceivably become more aware of conservation issues (Coe, 1985). Improved habitats should also address some of the concerns voiced by those in the animal rights and welfare community and should serve to lessen their criticism of zoos, namely, that maintaining animals in barren, unnatural enclosures is inhumane.

Another trend in contemporary zoos is that many are increasingly less willing to exhibit single individuals representing large numbers of different species, or what has been criticized as a postage stamp approach to collection diversity, something that was common during the early years of zoo history (Brambell & Mathews, 1976). Increasingly, zoo managers are concentrating on more relevant social groupings of animals, often necessitating a reduction in the number of different species being displayed. Further, zoos are more and more likely to be organized zoogeographically, so that there is some legitimacy to the juxtaposition of species in the zoo (Hancocks, 1978).

The more advanced enclosure designs address the necessity to secure animals for medical and observational procedures. Thus animal medicine, husbandry, behavior, ecology, and other components of the long-term maintenance of animal populations must be considered when new exhibits are designed. Architects must be educated about the requirements of modern zoos, not the aesthetics of traditional architecture.

As animal populations declined in the wild, it became clear that zoos would need to increase the survival rate and reproductive success of their animals, if only to replace those lost on exhibit. Hence, in contemporary zoos, captive propagation is one major focus of zoo research. While most managers of captive animal populations acknowledge that they are preserving a mere vestige of species that may soon cease to exist in the wild, many hope that zoos are functioning as buffers that will retain a reservoir of genetic diversity until such time as rampant environmental degradation can be reversed (Western, 1986). At that time zoo animals might provide founding populations for areas where they had once existed. Since species, not individuals, are what are important in the long term management of animal populations and species have arisen through complex interactions with specific environments over time, the inability to replicate natural habitats in captivity implies that long-term captive management schemes are, at best, measures of last resort.

In order to preserve genetic diversity, better systems for managing the breeding of limited captive populations of animals are being developed. These include the use of stud books, a system of recording genealogy of animals born in zoos; the International Species Inventory System (ISIS), a computerized data base enabling zoos worldwide to maintain records on the pedigrees of their animals; and species survival plans. ISIS facilitates optimum pairing of captive animals, many of which exist at population levels near the theoretical thresholds thought to be necessary to maintain adequate genetic diversity. Species survival plans have been designed for many taxa and address the long-term strategies for maintaining captive populations in zoos, ultimately envisioning reintroduction into their former habitats (Mallinson, 1984).

The requirement that sufficient numbers of animals be housed in captivity until prospects for survival in the wild improve implies that some limit be placed on the number of individual species represented in zoos. Conway (1974) suggests that the present carrying capacity of all of the world's zoos can support only three hundred and thirty species of mammals at levels sufficient to maintain adequate heterozygosity. This number of species limits the population of any one species to between two hundred and fifty and three hundred individuals. At these levels, 90 percent of the heterozygosity derived from the wild genotype can be maintained for twenty years. If, for example, the more than two hundred species of primates were maintained at these levels in the world's zoos, there would be no space for any other representatives of endangered fauna--and, would cost more than $50,000,000 annually (Conway, 1974).

Despite their spatial and financial limitations, modern zoos are becoming more important as laboratories for research by students and faculty of local universities representing the fields of psychology, ethology, zoology, and behavioral ecology. The involvement of universities in the monitoring of animal behavior in zoos has been advocated for decades (Snyder, 1975) and is only recently being emphasized by animal behavior researchers. This emphasis on behavior represents a dramatic shift from the primary type of zoo animal research that occurred during the first half of the 20th century, the post mortem (Snyder, 1975). While this investigation into mortality was important, it no longer constitutes the primary avenue of investigation in zoos.

The modern zoo offers the contemporary behavioral scientist the opportunity to observe a diversity of fauna in relatively confined settings, combining aspects of the work of classical ethologists with that of traditional comparative psychologists (Snowdon, 1983). The combination of an evolutionary perspective and the tighter degree of control available in a zoo, as compared to an observational field study, benefit both the scientific and conservation communities.

Data acquired by ethologists in the field could be compared to those obtained by comparative psychologists on the same species in zoos to assess the influence that captivity exerts on behavior. Variation in the range of responses to specific manipulations can be investigated (Altmann, 1967; Mason, 1968). These data could suggest techniques for improving captive habitats and management strategies. This approach to the study of animal behavior in captivity will be facilitated even more as habitats become increasingly representative of the habitats wherein the ancestors of captive animals evolved. This possibility for the union of the approaches of ethology and comparative psychology suggests that zoos can provide a venue for the resolution of the historical schism that has existed between these two disciplines (Mason & Lott, 1976), with both the scientific and conservation communities reaping the benefits of such a resolution.

Implications of Environmental Enrichment

The importance of the physical environment to captive animals has been suspected for several decades (Hediger, 1964/1950) and continues to generate discussion (Hutchins, Hancocks, & Calip, 1978; Markowitz, 1982). The restricted environments typically found in zoos have been associated with stereotyped locomotor behavior, depressed activity levels, poor reproduction, self inflicted injury, and abnormal behaviors, such as coprophagy (Clark, Juno, & Maple, 1982; Meyer-Hozapfel, 1968). Rowell (1972) reported that captive primates often exhibited elevated levels of aggression toward, and food competition with, conspecifics in confined, unnatural habitats. In addition, the close confinement of numerous animals probably resulted in olfactory and auditory hyperstimulation, although little research has been done in these areas.

Captive environments which do not allow animals to interact normally with conspecifics--or to engage in complex problem solving while contending with variation in the physical properties of the environment--could have profound implications for the health of individual animals and for the long-term viability of populations of endangered captive animals.

The rationale underlying environmental enrichment is based on the concept that organisms have been prepared through phylogeny for a specific range of ontogenetic expectancies. In artificial habitats, for ontogenesis to proceed normally, environmental contingencies must approximate those likely to have occurred in the wild over many generations.

Habitat improvement traditionally has been represented by two strategies, the naturalistic approach (Hutchins, Hancocks, & Calip, 1978-1979), often employing passive solutions that mimic aspects of natural habitats; and a more technological approach (Markowitz, *et al.*, 1978), often employing interactive solutions to create more variable zoo habitats. A more contemporary approach envisions an integration of both types of habitat improvement, enabling captive animals to interact with ecologically relevant variation in their surroundings (Forthman-Quick, 1984).

The more closely an artificial habitat resembles that from which an animal has been removed, the less likely newly captured animals are to experience the high rates of mortality that they often exhibit. Further, ecologically valid artificial habitats are less likely to subject captive animals to artificial selection. Unfortunately, in some cases, behavior which is not adaptive in the wild facilitates more efficient captive maintenance. There is an initially severe selection against easily aroused newly captured individuals, i.e., those that would probably survive most successfully in nature. Animals unable to habituate readily to the presence of caretakers are often injured in attempts to avoid human interaction and experience a high rate of mortality when first brought into captivity (Meyer-Holzapfel, 1968). Hediger (1964/1950) has advocated habituation of animals to their keepers as a husbandry strategy to mitigate levels of arousal. Mellen (1991) reports that reproductive success in small exotic felids is correlated with a more interactive husbandry style. Unfortunately, captive animals which characteristically demonstrate reduced wariness would probably not survive reintroduction to the wild.

The quality of the habitat exerts profound influences on the physiology and anatomy of captive animals. Current research suggests that information from the environment can modulate neural development and reduce the degradation of the central nervous system (CNS) often associated with aging (Coss, 1985). Studies that focus specifically on these effects in inbred rats further suggest that these effects may be exacerbated in limited captive populations.

Sensory information from the environment modulates neural development by altering the pattern of synaptic connections in the central nervous system. The CNS and sensory systems of a species are selectively responsive to salient environmental input--critical for their growth and development (Coss, 1985). For example, the relationship between the effects of unresponsive environments on neural development and ontogeny of behavior in laboratory rats has been demonstrated (Greer, Diamond, & Tang, 1982). This research demonstrates that there is a positive correlation between environmental complexity and numbers and development of neurons, dendrites, and dendritic spines, especially in immature animals. However, even older animals introduced to more complex environments exhibit a reduction in the rate of senescence of the CNS typically associated with traditional captive habitats. (Greer, Diamond, & Tang, 1982).

Other studies have investigated the influence of environmental complexity on the brains of male homozygous Brattleboro rats. These animals are deficient in vasopressin, which is correlated with an accelerated turnover rate of norepinephrine and a concomitant increase in the catabolic activity in some regions of the brain. Homozygous rats exhibited a more pronounced reaction to environmental enrichment than did heterozygous rats, as measured by changes in cortical thickness. Homozygotes, when housed in more complex surroundings, exhibited significantly greater increases in the size of the subcortical telencephalon, caudal encephalon, and hippocampus compared to the brains of heterozygous rats housed in similar surroundings. In unenriched habitats, homozygous rats responded more negatively than their heterozygous counterparts, based on the same cortical measures (Greer, Diamond, & Murphy, 1982).

Greer, Diamond, and Tang (1982) suggest that enrichment procedures might have differentially influenced the homozygous group by decreasing the catabolic breakdown of norepinephrine, resulting in increased synaptogenesis. Norepinephrine has been implicated as a neural hormone that facilitates anabolic activity throughout the central nervous system. Homozygous rats are smaller and are more easily aroused than heterozygous rats. Elevated arousal is correlated with increased sympathetic and catabolic activity in the central nervous system. Possibly, under enriched conditions, increased adrenergic activity reduces sympathetic activity and its attendant catabolic and associated systemic stress responses.

These effects were more extreme in older animals; in impoverished habitats, homozygous strains exhibited more rapid deterioration in the CNS with age than heterozygous rats. In enriched surroundings, the differences between the two groups decreased, i.e., homozygous animals appeared to respond more positively to improved habitats than heterozygous animals (Greer, Diamond, & Tang, 1982). Apparently, enrichment procedures can ameliorate metabolic influences on central nervous system abnormalities in inbred animals. Whether or not these same effects occur in other species is not currently known.

What is known is that many captive animal populations are inbred and becoming increasingly homozygous (Kear, 1977) and could be extremely susceptible to the influences of environmental impoverishment. Further, animals typically achieve longevity in captivity seldom realized in the wild. While enrichment schemes are most effective in young animals, e.g., by influencing the proliferation of proximate dendritic branches, there is still some improvement in the preservation of distal branch morphology in very old animals (Connor & Diamond, 1982). Consequently, enrichment procedures can be applied to old animals as well as young animals with some positive results.

Homozygous reactivity to environmental enrichment, even in older specimens, could allow inbred animals to be maintained for extended periods of time in neurologically robust condition. Homozygous or not, rats exposed to environmental complexity throughout their lives show reduced dendritic spine retraction (greater retention of dendritic spines) with age when compared to rats reared in less responsive environments. Specifically, their layer 3 neurons, which receive the primary afferent input from the lateral geniculate nucleus, show the greatest response to rearing conditions. Dendritic complexity in this layer is correlated with visual complexity in the surroundings, which is further correlated with the rate of firing of cortical and thalamic neurons, implying that neuronal activity is necessary for the maintenance of dendritic structure (Greer, Diamond, & Murphy, 1982). This proposed mechanism demonstrates that the visual richness of an animal's surroundings affects the degree of cortical complexity. Whether similar mechanisms operate in the auditory realm is not currently known. It is, however, conceivable that the provision of habitats with increased auditory complexity could exert similar beneficial influences on the auditory cortices of captive animals. In addition to positive effects on the CNS, enriched habitats exert beneficial influences on the overall health of captive animals. Provision of complex substrates and appropriate vertical complexity can influence the musculoskeletal health of captive animals by encouraging species-specific locomotor behavior. Another benefit of increased activity is that deviations from normal behavior can be more easily detected. Since wild animals tend to disguise any injury or disorder, changes in normal locomotor behavior can be used to monitor the health status of animals (Markowitz, 1982). Significant deviation from typical behavior might indicate an injury that should be investigated by zoo veterinarians (Markowitz, Schmidt, & Moody, 1978).

Traditionally, schemes that were designed to improve habitats concentrated primarily on increasing the amount of space available to animals (Hediger, 1964/1950). Often habitats were landscaped to appear more natural to observers, i.e., more naturalistic (Hutchins, Hancock, & Calip, 1978-1979). Increased apparent naturalism in an exhibit certainly reduced the sterile appearance of traditional enclosures. Nonetheless, the issue of behavioral opportunities for captive animals was seldom addressed by these relatively passive improvements. Consequently, a more interactive approach to improving captive habitats emerged, one exploiting contemporary advances in technology.

An unfortunate schism arose between the advocates of the two fundamental approaches to habitat improvement. Advocates of behavioral enrichment suggested that exclusively naturalistic approaches to habitat improvement did not adequately address the unresponsiveness of sterile environments (Markowitz, 1982), while critics of behavioral engineering asserted that the imposition of artificial devices into the surroundings of captive animals was unnatural and inappropriate. For many years, the advocates of each strategy appeared to be in contention for legitimacy within the zoo community. Fortunately, this controversy has subsided with the proposal for an integrated approach to the improvement of zoo habitats (Forthman-Quick, 1984). This integrated approach advocates a blend of both strategies. While habitats should appear as natural as possible, they should also be responsive to the animal. In some unfortunate instances, inadequate enclosures can not be structurally improved; the most effective approach in these instances is to retrofit enclosures with interactive equipment. As far as appearances are concerned, this can make a bad situation worse. Those who object to the installation of unnatural looking devices can be placated by the use of natural looking materials to disguise interactive equipment.

Oddly, the objections raised by some over the introduction of technology into zoos are probably spurious. Most major advances achieved in zoos over the past few decades have been based almost entirely on the application of modern technologies to meet zoo requirements.

Another arena of controversy concerns the perceived level of intervention claimed by some to occur under enrichment procedures (Hutchins, Hancocks, & Calip, 1978-1979). This is an odd objection to behavioral engineering when one considers that the removal of an animal from nature is the most profound form of intervention possible. Perhaps some researchers object to the notion that, under some enrichment strategies, animals are being forced to work for sustenance. This contention is not supported by the classic research of Carder and Berkowitz (1970), which suggests that animals will interact with an apparatus even in the presence of ad libitum food--not a surprising finding in view of the fact that wild animals spend most of their time foraging and avoiding predation (Hediger, 1950/1964).

Certainly, the introduction of technology into enclosures is not the only means by which captive habitats can be improved. Other aspects of the environment which can be modified in ways that improve the conditions of captivity include the provision of proper social environments reminiscent of those observed in the wild. Proper social surroundings can provide an interactive environment facilitating social learning (Mason, 1965). In inadequate social surroundings, where adequate social development is impossible, several types of stereotypies can develop, including excessive autogrooming, self-clasping, and other repetitive infantile behavior patterns (Meyer-Holzapfel, 1968; Mitchell, Maple, & Erwin, 1979).

Other aspects of habitats that can be easily improved include the quality and quantity of space (Maple & Finlay, 1986). The effective size of an enclosure can be increased by augmenting the horizontal substrate variability and vertical complexity, e.g., by introducing climbing structures, ledges, and vegetation. Greater vegetative complexity allows arboreal species to engage in important locomotor activities that can be inhibited in artificially simplified surroundings. Wendt (1979) reports that free living cotton-top tamarins exhibit more arboreal leaping than captive individuals. In fact, these animals often leap over distances of three meters, greater than the space available to them in most artificial habitats, probably accounting for the low level of arboreal leaping observed in captive tamarins. The usable space should also be sufficient to allow animals to obtain cover and maintain minimal critical distances from one another (Hediger, 1964/1950).

The provision of adequate buffers between zoo visitors and animals must also be considered. Many contemporary zoo habitats are constructed with plexiglas or perspex sides and feature reduced buffer distances between visitors and animals. The decreased distance between animals and visitors suggests that enclosures be designed with adequate space or cover to allow animals to withdraw from interactions with visitors. This can be accomplished by increasing the complexity of the substrate or vegetation within the enclosure.

Substrate improvement does not require that the physical size or structure of the enclosure be altered; the quality of the available space appears to be more important than its quantity (Erwin, 1986).

Naturalistic substrates, e.g., straw, can be employed to provide variability within the enclosure and manipulatable objects can be distributed ad libitum to encourage investigatory behavior in dexterous species (Westergaard & Fragaszy, 1985). This approach has been successful with capuchin monkeys, where, while the provision of this form of substrate reduced excessive passive affiliative behavior, the level of play and grooming were not reduced; animals developed innovative behaviors through individual experience (Westergaard & Fragaszy, 1985).

In a study of foraging strategies in saddleback tamarins, Menzel and Juno (1985) reported that naturalistic testing conditions, including substrates, and ecologically relevant stimuli improved the object learning and memory performance of their subjects, surpassing the performance of animals tested in more traditional surroundings. This finding illustrates the importance of ecologically relevant surroundings in encouraging the full range of expression of a species' behavioral potential.

Many species exhibit elevated levels of aggression when confined in habitats with insufficient area, often the case in zoos and laboratories (Erwin, 1986). Epple (1975) maintains that levels of aggression increase in common marmosets, saddleback tamarins, and Geoffroy's tamarins when space requirements are not met; there was also a report of at least one instance of fighting to the death in a pair of yellow-handed tamarins.

Available space is only one of many environmental parameters which influence levels of aggression in captive animals. Cotton-top tamarins, housed in typical zoo environments, show a reduction in affiliative behavior and an increase in agonistic behavior compared to those housed in laboratory environments (Glatson, *et al.*, 1984). In the zoo habitat, animals exhibited more affiliative behavior, e.g., allogrooming, in the morning than in the mid-day, a finding implicating the presence of zoo visitors as an influence on social behavior. There is a significant negative correlation between the average number of zoo visitors and the frequency of affiliative behavior, while that between the number of zoo visitors and the frequency of agonistic behavior is positive. Aggression between isosexual parents with their offspring is also greater in the zoo environment than in the laboratory, a critical problem for a species whose parenting abilities are transmitted socially. These findings could have profound implications for zoos attempting to simultaneously display and successfully breed cotton-top tamarins (Kirkwood, 1983; Brand, 1981).

One broad area of sensory experience often overlooked in the design of captive habitats is the acoustic environment, the focus of this study. The unnatural acoustic surroundings in which animals are usually housed could elevate levels of stress through acoustic hyperstimulation or, in some species, prevent the acquisition of normal adult vocal repertoires.

While some species are able to emit species-specific vocalizations immediately after birth and exhibit some competency in vocal behavior even if reared in inadequate environments, e.g. talapoin monkeys and squirrel monkeys, other species probably require immediate feedback from their own vocal activity and vocal interaction with conspecifics throughout ontogeny in order to perfect the adult vocal repertoire. This is particularly important in species featuring geographically- and troop-specific dialects (Marler, 1985). Troop-specific dialects have been observed in Japanese macaques (Green, 1981) and mustache tamarins (Snowdon & Hodun, 1985). Some species appear to demonstrate vocal behavior suggesting the presence of vocal learning, which is critically dependent on adequate social environments. Immature cotton-top tamarins emit contextually inappropriate vocalizations. This variability in vocal behavior is reduced as the animals mature but only if animals are placed in a proper social environment. This form of gradually improving vocal behavior has also been observed in the field in young vervet monkeys (Seyfarth, *et al.*, 1980). Only after experience in the emission of various alarm calls within different contexts do young monkeys acquire adequate skill in vocal behavior. Immature pygmy marmosets which have been removed from their parents never develop a fully functional adult vocal repertoire (Snowdon, 1986).

There are both genetic and experiential factors in the acquisition of normal adult vocal behavior. Providing an adequate social environment featuring the vocalizations of conspecifics can provide the proper social feedback necessary to allow for the maturation of species specific vocal repertoires. Conversely, artificial habitats featuring minimal acoustic complexity might inhibit the development of normal adult vocal behavior.

The provision of acoustically variable habitats might also facilitate the development of the abilities of immature captive animals to localize important sounds in their surroundings. Knudsen (1984) reported that young animals require the opportunity to practice sound localization throughout development in order to develop the perceptual and motor skills required to engage in this class of behaviors adequately as adults. As young animals mature, the sound shadow produced by the head and the inter-aural distance increase to typical adult values, increasingly facilitating the reception of ecologically important acoustic phenomena.

The experience that an animal obtains throughout development affects other aspects of the manner in which it responds to its surroundings (Mason, 1965). Rhesus macaques reared in social isolation display poorly developed social competence, characterized by an inadequate social repertoire. As adults, poorly developed social competence inhibits successful reproduction. Hence, captive habitats must accommodate the behavioral requirements of animals at all stages of their development (Sackett, 1968). Hand reared Callitrichids, especially those which have never interacted with conspecifics, display inadequate parenting skills, resulting in high rates of infant mortality (Collier, Kaida, & Brody, 1981). Ultimately, it is the restriction in social and sensory experience that results in abnormalities in locomotor activities, reductions in exploratory behavior, social incompetence, and increased aversion to complex novel stimuli. For example, social deprivation throughout the first six months of life in rhesus macaques is irreversible. If, however, animals are introduced to more socially complex surroundings early enough, animals can exhibit nearly normal social behavior as adults (Sackett, 1968).

With many captive animals, especially those which have been hand reared, there appears to be a retardation of maturation. Artificially reared animals often exhibit persistent juvenile behavior patterns, a disturbing trend for individuals representing endangered species required for future breeding programs. For example, captive Geoffroy's tamarins exhibit persistent infantile gestures, crouching, freezing, and vocalize more frequently with submissive 'twitters' than parent-reared or free-living tamarins (Moynihan, 1970).

Inadequate habitats and husbandry techniques probably result in inadequate social development and, ultimately, increased reactivity, indicative of increased stress. The consequences of elevated stress or improper socialization have profound implications for the managers of captive primate populations. Among the most important of these implications is an almost universal increase in intra-specific aggression--with the increased probability of injury to valuable animals. This problem is exacerbated in artificially simplified habitats which do not enable animals to regulate their distances from and interactions with one another (Erwin, 1986). Adequate spatial complexity and quantity which allow animals to partition the habitat can reduce aggressive interactions. For example, Callitrichids appear to show elevated levels of aggression in laboratory settings where animals are unable to avoid interacting with one another (Epple, 1975). To the extent that zoo habitats are similar to laboratory settings, elevated levels of aggression can pose management problems. Among the most important of these amenable to improvement through behavioral enrichment is the moderation of stress in captive animals.

Stress in Captive Animals

One of the primary reasons for providing improved habitats for captive animals is to reduce levels of arousal, as measured by reactivity, possibly indicative of elevated levels of stress (Stoskopf, 1983). The regulation of stress, as measured by its physiological consequences, is fundamental to the contemporary paradigm of behavioral enrichment. Stress is an organismic response often correlated with environmental factors over which an animal has no control. It is characterized by psychoneuro-endocrine influences on the physiology and behavior of an organism through its neuroendocrine axis (Stoskopf, 1983). Increased reactivity, stereotypical behavior, and aggression are possible indicators of elevated levels of stress. Hypothetically, stress should be reduced if animals are provided with some means of influencing their surroundings.

Chronic stress is thought to be an important causal factor in the high rates of mortality observed in some captive animals. Prolonged over--stimulation of the autonomic nervous system is correlated with increased activity in the hypothalamic-adrenal system. Increased levels of epinephrine, metabolic rate, blood pressure, and tachycardia are all associated with elevated levels of arousal and stress (Snyder, 1975). Elevated levels of arousal are artifacts of the fight-or-flight syndrome and are adaptive in the wild (Stoskopf, 1983). However, when wild animals are introduced into captivity, continually elevated levels of arousal can compromise their health.

Some behavioral correlates associated with elevated levels of stress include reduced foraging, reduced locomotor behavior, impaired reproduction, and increased eliminative behavior (Stoskopf, 1983). Animals exhibiting behavioral signs of stress often possess elevated levels of adrenal corticosteroids. These hormones are released by the adrenal cortices in response to the release of adrenocorticotropin hormone from the anterior pituitary (Rowell, 1972). The efficiency of the immune system can be impaired by constant exposure to stressful conditions. Chronic elevation of corticosteroid levels inhibits the function of activated B-lymphocytes and can result in a reduction in antibody production. Reduction in the efficiency of primary immune systems can increase the susceptibility of animals to infection (Snyder, 1975; Stoskopf, 1983). Extended periods of elevated levels of cortisol can result in the reduction of many biochemical cofactors, e.g., nicotine adenine disphosphonucleotide (NADPH)--important in several detoxification pathways, and a reduction in intracellular ion concentrations, including calcium and magnesium. Female animals can respond to stress with elevated levels of follicle stimulating hormone, prolonged estrus, and premature parturition. Males can respond by showing atrophied testicles or Leydig cell nuclei, resulting in reduced rates of spermatogenesis (van Hooff, 1986). Adrenocorticotrophic hormone (ACTH) is adaptive in nature because it enables animals to rapidly mobilize energy in emergency situations. However, prolonged periods of exposure to elevated levels of ACTH can negatively affect reproduction, blood clotting, and the suppression of systemic infections (Snyder, 1975).

Typical stressors characteristic of captive settings include: the presence of ecological adversaries (especially humans), inadequate social settings, overcrowding, restricted opportunities for movement, inappropriate substrates which do not provide adequate opportunities to obtain cover, inadequate diet, and inappropriate abiotic environmental characteristics, including temperature, humidity, and photoperiod (Snyder, 1975; Stoskopf, 1983). Additionally, captive animals are often surrounded by unnatural acoustic environments (Gamble, 1982).

There is considerable variability between species in the manner and magnitude of response to the unnatural conditions of captivity. Those species which demonstrate extreme reactivity to the presence of human beings are disproportionately likely to be injured during attempts to avoid interactions with caretakers and observers (Meyer-Holzapfel, 1968). Hediger (1964/1950) has advocated taming reactive animals by invoking regimens of training which familiarizes animals with those individuals with whom they engage in regular contact. Familiarization should reduce the stressful effects of the presence of humans and even the sudden changes in the physical surroundings that they often impose upon their charges. This approach to reducing reactivity has been found to be effective with some difficult to breed species, e.g., many exotic felids (Mellen, 1991). Unfortunately, this approach might prove to be counterproductive in species targeted for re-introduction into habitats from which they have been extirpated. The provision of adequate and appropriate space can ameliorate stress in captive animals (Rowell, 1972). Unfortunately, enclosures which are designed for maximum hygiene and ease of maintenance are characterized by sterile, invariant substrates. Animals housed in this type of enclosure can seldom avoid constant interaction with cagemates--nor escape from visual contact with human observers. In some species, e.g., many cercopithecines, this situation can result in elevated levels of intragroup aggression. In order to adequately satisfy minimal space requirements, an amount of space equivalent to an area circumscribing a species-specific area around each individual should be provided for within each enclosure. This minimum area, termed the flight distance, has been discussed extensively by Hediger (1964/1950).

Another important spacial characteristic to be considered in the management of stress is the complexity of space, which can determine the amount of cover available to animals.

Failure to consider any of the above features of the physical habitat can induce chronic stress in captive animals. Increased stress, as measured by elevated levels of arousal, is often correlated with increases in the rates of otherwise normal behaviors. For example, Callitrichids characteristically feature high basal levels of scent marking, which, nonetheless, significantly increase when animals become aroused (Epple, 1985). Unfortunately, this otherwise useful indicator behavior is influenced by regular cage cleaning procedures, which remove previously deposited scent marks. In response to cleaning, animals usually attempt to reanoint their surroundings (Hediger, 1950). The resulting increase in the rate of scent marking confounds the use of this behavior as a behavioral index of arousal.

Another potential stressor found in most artificial habitats is an unnatural photoperiod. Traditionally, animals housed in artificial habitats, especially those transported from the neotropics, have been subjected to the photoperiods characteristic of the region near the destination institutions, or have been subjected to artificially controlled photoperiods, typically twelve hours of light alternating with twelve hours of darkness. The influence of artificial or unnatural lighting regimens on activity cycles, social behavior, or reproduction are often ignored (Erkert, Nagel, & Stephani, 1986), even though their modulation of diurnal activity patterns through the suprachiasmatic nucleus has been understood for some time (Hoban & Sulzman, 1985; Hobbs, 1981).

Photoperiodicity is important in regulating reproduction in many photosensitive species, including Callitrichids. Artificial light cycles can impede reproduction directly by interfering with photoperiodic cues that prime animals for reproduction or by increasing their levels of systemic stress (Snyder, 1975). Species-specific differences in responsiveness to specific kinds of habitat improvement are often dramatic. Those species that exhibit a strong social attachment to conspecifics will respond poorly to other types of habitat improvement in the absence of an adequate social environment. For example, titi monkeys are monogamous and form strong pair bonds, while squirrel monkeys are polygynous and form looser associations. When titi monkeys are separated from cage mates, they exhibit more apparent distress than do squirrel monkeys. Squirrel monkeys appear to engage in considerable competition for enrichment devices, while titi monkeys demonstrate more social cooperation in exploratory behavior. Titi monkeys housed in pairs exhibit higher rates of exploratory behavior than those housed individually, while squirrel monkeys housed individually exhibit higher levels of exploratory behavior compared to those housed in groups--especially if dominant individuals are present (Fragaszy & Mason, 1978).

These species also differ in their physiological response to the presence of other animals. Housing arrangements which interfere with the ability of monogamous titi monkeys to interact with one another result in changes in physiological parameters suggestive of elevated levels of stress (Mendoza & Mason, 1986). Even though baseline adreno-cortical activity is higher in squirrel monkeys than in titi monkeys, titi monkeys respond more strongly to the presence of isosexual animals than do squirrel monkeys. In fact, female squirrel monkeys exhibit a reduction in cortical activity when introduced to an isosexual stranger, even though they have higher baseline levels of, and exhibit greater fluctuations in, the levels of cortisol compared to titi monkeys. These differences in reactivity appear to be correlated with the different social systems of the two species (Mendoza & Mason, 1986). This work illustrates the importance of considering the social system of a species when designing housing or when groups of animals are manipulated for research.

One important aspect of artificial habitats which seldom receives attention from designers and managers of zoos and laboratories is the acoustic environment. In modern facilities there are relatively high levels of unnatural noises generated by automated equipment, caretakers, and visitors. Automatic systems of every description, motorized vehicles, communications equipment, and their operators produce noise that surrounds captive animals. Elevated sound pressure levels have been shown to exert deleterious effects on many species of laboratory animals (Gamble, 1982). In some species, the nearby presence of aperiodic, intense, unnatural sounds can effect the baseline levels of many behaviors (Stoskopf, 1983).

Constant sounds, or those with a periodic nature can subtly influence the physiology of some particularly sensitive species. Van Rooijen (1984) has discussed this problem in the context of tape playback studies, noting that periodicity and amplitude are parameters that are not sufficiently considered when playback studies are designed.

Sound can be an important factor in the development of some pathologies in captive animals. Excessively loud sounds are correlated with audiogenic seizures in inbred strains of mice increased adrenal weight and arousal levels as measured by startle responses in rats and decreased levels of grooming and other maintenance activities in many rodents (Bevan, 1955, cited in Gamble, 1982). Chinchillas exhibit a demonstrable loss in auditory acuity when exposed to the sounds of machinery at pressure levels of 65 dB to 105 dB for periods ranging from two to two hundred and twenty one days (Carder & Miller, 1971, cited in Gamble, 1982). Rhesus macaques exposed to the sounds of jackhammers show a decrease in overall locomotor activity and increases in clasping and huddling after only one hour of exposure ("Primate Record", 1973, cited in Gamble, 1982). Lactating tree shrews exhibit a marked reduction in milk production in response to unnaturally loud sounds (D'Souza & Martin, 1974, cited in Gamble, 1982). These findings suggest that attempts should be made to reduce the sources and intensities of unnatural sounds in animal care facilities. Further, attempts should be made to replicate the acoustic profile of an animal's natural habitat.

The premise that the provision of more interactive, ecologically relevant housing will reduce stress levels and improve the health of captive animals is the primary rationale for improving artificial habitats. The degree to which habitat modifications have been successful can be difficult to quantify. One commonly applied measure of the success of housing conditions and maintenance regimens is reproductive success. Unfortunately, even between closely related taxa, there are large differences in reproductive success, reducing the general applicability of successful solutions. For example, the common marmoset appears to be less reactive than many other Callitrichids, e.g., cotton-top tamarins as suggested by its better reproductive performance in captivity (Ogden, Wolfe, & Dienhardt, 1983).

The zoo environment exerts profound influences on the behavior and physiology of its animals and can affect the long term prospects for the successful management of captive animal populations. It can encourage or discourage the development, expression, and, ultimately, possibly the retention of important behaviors, including those involved in defense, communication, and reproduction.

While field studies can illuminate aspects of the ecology and behavior of free-living animals, the ability to view exotic animals at close range provides unique opportunities to improve our understanding of the influence that captivity exerts on behavior. Differences in responsiveness to environmental variation are the norm; captive management and behavioral enrichment schemes should be designed with a thorough knowledge of the natural histories of target organisms, including their mating and social systems, reproductive physiologies, and systems of communication, in order to realize the greatest improvement in prospects for future survival in captivity.

The Natural History of the Callitrichidae

Evolution, Taxonomy, and Morphology

Primate fossils have been discovered in South America that are 20 million years old, suggesting deposition during the Eocene. Eisenberg (1981) states that Callitrichids diverged from a common Cebid ancestor during the Oligocene, while tamarins are thought to have diverged from a common Callitrichid ancestor during the late Pleiocene. The different species might have become geographically and consequently reproductively isolated when inland seas formed during this period. The remnants of these bodies of water are still found in the region of the Rio Magdalena Cauca and the lower Rio Acaco.

The taxonomy of the Callitrichidae is contentious and confusing (Herskovitz, 1977; Kleiman, 1985). Callitrichids are classified within the order *Primates*, in the suborder *Anthropoidea*, and within the infraorder *Platyrrhini*. They are further assigned to the superfamily *Ceboidia*, comprising the New World primates, including the families Callitrichidae and *Cebidae* (Bramblitt, 1976). Some authors assign both the *Callitrichidae* and *Callimiconidae* to the superfamily *Callitrichinae* (Napier & Napier, 1985), adding to the confusion. The Callitrichids are organized into four genera, *Cebuella, Callithrix, Saguinus*, and *Leontopithecus*.

The derivations of many of the names assigned to Callitrichids include their habitat types, food preferences, and anatomical peculiarities. For example, the pelage of virtually all members of the family is striking and often provides the source material for the precise scientific name. Some authors, usually Europeans, employ the term Callithricid, as opposed to Callitrichid. However, Hershkovitz (1984) suggests that the former usage is incorrect, that Callitrichid is more nearly equivalent to the root word from which the family name was derived; Callitrichid literally means 'beautiful hair'. The term *Saguinus*, or the European *sanguinous*, appears to have been derived from the term for blood or fluid feeding, probably because some Callitrichids--especially *Cebuella spp.*--actively exploit the exudates of plants. The term *marmoset* appears to date back to Middle English and could have arisen from the French *marmousett*, meaning grotesque human (Walker, 1975). The term *tamarind* might have been derived from a Baroque French word for a genus of South American tree, the *Tamarinde,* in which Callitrichids had been observed feeding by early European explorers. The precise species appellation for the cotton-top tamarin, *oedipus*, was probably inspired by their relatively large feet and suggests that these resemble the club foot condition of the Greek tragedy's king (Wendt, 1979).

The *Platyrrhinae* are distinguished from the *Catarrhinae* by the presence of a broad rhinarium with laterally displaced nostrils, hence the term *Platyrrhine* (Bramblett, 1976; Hershkovitz, 1977). Only in the New World *Cebidae* are there found prehensile tails. Callitrichids possess a suite of typical primate characteristics, including a relatively large ratio of central nervous system to peripheral nervous system mass (although the cortex is comparatively smooth), forward facing eyes fully enclosed in a bony orbit, well developed stereoscopic vision, a more ventrally located foramina magnum, well developed vestibular control, highly developed appendicular control, a well developed precision grasp, and a prolonged developmental period (Napier & Napier, 1985).

Traditionally, Callitrichids have been described as possessing

primitive morphologies compared to other primates (Hershkovitz, 1977). Some contemporary researchers suggest that many characters usually indicative of primitive morphologies are actually secondarily derived and represent a suite of adaptations characteristic of phyletic dwarfing (Ford, 1980). Some characters thought to represent a primitive state include their small size; all Callitrichids weigh less than 800 g and are less than 60 cm in total body length (Kleiman, 1978); the presence of twinning; a simplified dental formula, including the absence of third molars and the presence of tritrabecular upper molars; an emphasis on olfaction, including an active vomeronasal organ; an incompletely ossified middle ear canal; and radially arranged claws or tegulae on all but the hallux, i.e., the first digit (Moynihan, 1976). However, Ford (1980) contends that what appear to be traits reminiscent of the primordial *Platyrrhine* ancestor are advance characters, and are derived rather than conservative traits.

Hershkovitz (1977) advocates the view that increasing body size is representative of evolutionary advancement, and that small body size represents a primitive character. This view is not supported by data gathered from island dwelling species, where a decrease in body size is an adaptation to limited resources. Since smaller forms have reduced resource requirements, larger numbers of individuals could survive in a confined area, tending to preserve genetic diversity (Moynihan, 1976).

It is possible that Pleistocene climatic oscillations caused the forests of South America to be broken into discontinuous tracts, essentially forming ecological units similar to islands. The resulting selection could have favored a reduction in body size in some animals, including Callitrichids. Consequently, small size is not a primitive character, but rather, a case of pleseomorphism, i.e., the retention of a primitive state (Eisenberg, 1981). All Callitrichids are diminutive; the pygmy marmoset is the second smallest of all living primates. Even the largest Callitrichid, the golden lion tamarin is smaller than any presently living Cebid. Fossil evidence indicates that the Callitrichid ancestor was larger than the largest extant Callitrichid, suggesting that small body size is a derived trait (Napier & Napier, 1985).

The relatively high reproductive capacity of many Callitrichids might be thought to represent a primitive character, though in view of the very specialized reproductive physiology of Callitrichids, it probably represents an adaptation to high levels of predation (Ford, 1980). Callitrichids possess a simplex uterus, and both ovaries release ova simultaneously, usually resulting in dizygotic twins, which are unique among primates (Ford, 1980).

Another unique Callitrichid character is the presence of twin pectoral mammaries which sometimes possess supernumerary nipples, a condition termed polymastia. In addition, male Callitrichids possess a baculum in the penis (Walker, 1975).

The dental formula of Callitrichids is also considered to represent a primitive state, featuring a simplified post-canine dentition. The dental formula is 2,1,3,2 X 4=32 (Napier & Napier, 1985; Went, 1979). The third bottom molar never erupts, probably due to the foreshortening of the jaw, a trend also observed in other Cebids. The finding that this process is advanced in Callitrichids and is less advanced in other Cebids suggests that the Callitrichids are not the stem line ancestor of Cebids. Although the third molar is crowded out, the total masticatory surface is preserved by the increased degree of hypercony in the two remaining molars. *Callithrix* and *Cebuella spp.*

possess tritrabecular molars, which are associated with high levels of insectivorous diets. Hence, when viewed from an ecological perspective, what appear to be primitive traits are probably adaptations to a specialized niche (Ford, 1980).

The presence of curved, claw-like nails on all but the hallux, the large first digit, is thought to represent an adaptation to a clinging and leaping mode of travel, similar to the locomotor behavior of arboreal squirrels. The presence of apical pads located ventrally to the distal phalynx suggests that they are unimportant in locomotor activity and that the claws are secondarily derived adaptations important in foraging (Sussman & Garber, 1981).

There is considerable homogeneity within the Callitrichidae. In evolutionary terms, the present condition of the taxon could be considered transitory. Many tamarins are obviously closely related and are often distributed sympatrically. The homogeneity of the basic form and simultaneous niche diversity within the family suggests a recent series of adaptive radiations (Hershkovitz, 1977).

Whether or not the Callitrichids represent advanced, phyletic dwarves or primitive primates is a controversy that could be resolved by studies of Goeldi's monkeys, an animal which appears to be intermediate between the Callitrichids and the Cebids. These animals are slightly larger than Callitrichids, retain the third molar, feature twin pectoral mammaries, and do not show twinning (Moynihan, 1976). The dentition and skull morphology of *Callimico* suggests an affinity with the Cebids, but its small size and the presence of claws suggests an affinity with the Callitrichids (Napier & Napier, 1985). These animals appear to be converging on either Callitrichids or Cebids, but the direction of the trend is not clear.

The family Callitrichidae consists of four genera: *Cebuella* (pygmy marmosets); *Callithrix* (marmosets) ; *Leontopithecus* (golden lion tamarins); and *Saguinus* (tamarins) (Napier & Napier, 1985). The Callitrichids are conceptually divided into the long tusked genera (*Saguinus* and *Leontopithecus*) and the short tusked genera (*Callitrix* and *Cebuella*) based on the relative length of the canines to the incisors. Long tusked species possess canines that protrude beyond the incisors, similar to carnivores, while short tusked species possess incisors that match the occlusal plane or are longer than the canines.

The long, procumbent incisors of marmosets represent an adaptation for tree gouging while foraging for plant exudates (Hershkovitz, 1977; Wendt, 1979). Within the family, all tamarins are consistently larger, possess longer limbs, and are better leapers than marmosets. *Callithrix* species feature average total body lengths ranging from 20 cm to 25 cm and average tail lengths ranging from 20 cm to 35 cm. *Saguinus* species feature average body lengths ranging from 21 cm to 32 cm and average tail lengths ranging from 30 cm to 42 cm. The average weights within the genus *Saguinus* range from 250 g to 560 g (Walker, 1975).

There are eleven species comprising the genus *Saguinus*, including: *S. midas* (yellow-handed tamarins); *S. niger* (black- handed tamarins); *S. mystax* (mustache tamarins); *S. imperator* (emperor tamarins); *S. labiatus* (red-bellied tamarins); *S. negriphones* (black-eared tamarins); *S. fuscicolis* (saddleback tamarins); *S. negricolis* (black-mantled tamarins); *S. bicolor* (pied tamarins); *S. oedipus geoffroyi* (Geoffroy's tamarins); and *S. oedipus* (cotton-top tamarins). The genus includes some of the most successful species of New World primates (Hershkovitz, 1977). The tamarins are divided into the hairy faced and bare faced tamarins, including the crested, bare faced tamarins. Bare faced tamarins derive this appellation from the high degree of depilation around the face, exposing blackish skin around the ears, nostrils, and lips (Hershkovitz, 1977).

The bare faced tamarins include the *Saguinus bicolor* group and the *S. oedipus* group. The *S. bicolor* group is thought to be more advanced than the *S. oedipus* group because of the greater degree of facial depilation and greater range of chromatic diversity. Both groups are thought to have arisen independently from the hairy-faced tamarins of upper Amazonia. The ancestral bare faced tamarins are thought to have spread along the eastern Andes Mountains and then west into northern Colombia. Presently all species are distributed north of the Amazon River.

The *S. oedipus* group includes three subspecies: the cotton-top tamarin (*S. o. oedipus*), Geoffroy's tamarin (*S. o. geoffroyi*), and the white-footed tamarin (*S. o. leucopus*) (Hershkovitz, 1977). Although the *S. oedipus* species assemblage has occasionally been treated as representing variants of a single species, there are important differences between the three animals. The most noted chronicler of the natural history of New World Primates, Philip Hershkovitz, has advocated constructing separate genera for the Geoffroy's tamarin and the cotton-top tamarin. Additionally, Moynihan (1970) advocates changing the name of Geoffroy's tamarin to the rufus napped tamarin because of the presence of a reddish brown nuchal mane.

All three subspecies feature differences in size, weight, coloration, pinnae morphology, cranial morphology, and dental morphology. Geoffroy's tamarin is the largest of the three subspecies, weighing from 486 g to 500 g (Dawson, 1978), while the cotton-top tamarin weighs somewhat less, averaging 410 g (Neyman, 1978), with a reported range of from 260 g (Walker, 1975) to 500 g (Hershkovitz, 1977; Neyman, 1978).

Cotton top tamarins exhibit some sexual dimorphism, with females weighing slightly more--434 g--than males--431 g. Sexual dimorphism is also apparent in total body and tail length, with females averaging 650 mm in length and males averaging 640 mm in length. The mean head to rump length is 235 mm with a range of 175 mm to 310 mm. The tail is slightly longer than the body, ranging in length from 250 mm to 440 mm (Walker, 1975). The average brain weight is 10.6 g in males and 8.8 g in females, which yields a range of 1.9% to 2.5% of the total body weight. The contributions of other organs to the total weight of the animal include: heart (0.62% to 0.78%), lungs (5.3%), liver and gall bladder (3.7% to 5.4%), and the gonads (0.34%).

Despite differences, all three species exhibit similarities, including some degree of cranial hypertrichy--the presence of specialized head plumage, reduced pinnae, darkly pigmented, relatively hairless facial skin, some degree of countershading characterized by a white ventrum and a rufus to black dorsum, long, slender limbs, elongated digits terminating in curved claws, and a long, non-prehensile tail (Hershkovitz, 1977; Moynihan, 1970; 1976; Napier & Napier, 1985; Walker, 1975).

The white-footed tamarin retains the greatest amount of facial hair and is considered the most primitive of the three subspecies, possibly most closely resembling the ancestral form. Both it and Geoffroy's tamarin are more similar to one another than either is to the cotton-top tamarin. However, in the length of their tails, Geoffroy's tamarin and the cotton-top tamarin bear a strong similarity to one another. The cotton-top tamarin possesses the least amount of facial hair and is considered the most advanced of the three subspecies. It also features the greatest degree of dichromacy as exemplified by whitish-yellow underparts. All three subspecies feature relatively small pinnae, compared to the size of the cranium. The white-footed tamarin exhibits the least amount of reduction in the size of the pinna, Geoffroy's tamarin exhibits an intermediate degree of reduction, and the cotton-top tamarin possesses the most reduced pinna of the three subspecies.

An evolutionary trend is suggested by this progression in the reduction of the pinnae and by the change in pelage from an infant pattern in white-footed tamarins to a normal adult pattern in cotton-top tamarins. There is an apparent trend toward increasing albinism, erythrism, and dilute melanism, exemplified by the progression from white-footed tamarins to Geoffroy's tamarins to cotton-top tamarins which reveals a de-emphasis of the wilder agouti pattern and an increasingly discrete patterning of color (Hershkovitz, 1977; Moynihan, 1970).

The brain case of *Saguinus oedipus* is the most highly developed of all tamarins (Hershkovitz, 1977). The cranium of all three subspecies features a highly domed frontal contour, well developed temporal ridges which converge frontally and diverge parietally and independent sagittal crests which converge with paired temporal crests. The nasal profile is slightly concave. The mandible is more primitive than those of other tamarins, featuring a triangular ventral border, compared to the more rounded configuration characteristic of other tamarins. There is a slight arching of the horizontal ramus and the angular processes are slightly inflected ventrally.

In the cotton-top tamarin, the skin of the temples near the sides of the crown to the anterior borders of the ears is bare or covered with a sparse layer of silvery hair. This contrasts sharply with the thick, long white hair of the crown and nape. This hair forms a flowing mane that originates on the forehead and continues along the mid-sagittal crest to the margins of the ears and to the nape of the neck. The black skin of the cheeks is usually bare, but sometimes covered with a fine layer of long, silvery hair. There are always suborbital bands of silvery hair from the corners of the eyes to the angles of the jaw. The ears are small, devoid of any hair, and feature lower dorsal laminae which are deeply margined or altogether absent. The dorsal coloration is a modified agouti pattern, with the color of the ventrum ranging from yellow to white. The distal portion of the middorsal hairs sometimes feature a subterminal pale band. The tail features a black dorsal surface with a reddish orange ventral surface. The distal portion of the tail is almost always more darkly pigmented than the proximal portion (Hershkovitz, 1977; Walker, 1975; Wolfheim, 1983).

In Geoffroyi's tamarins there is a midfrontal wedge shaped crest of relatively short, white hair that continues to the nape of the neck, merging into a buff colored mantle and mane which terminates at the interscapular region of the dorsum. The black skin of the face sometimes features a fringe of silver hair descending from the nostrils to the corners of the mouth. There is a slightly heavier fringe of buff colored hair extending from the corners of the eyes to the angle of the jaw. The dorsal coloration tends toward buff, the lateral portions of the body are grey, and the ventrum white. The grey hairs of the sides can form a dark ridge that divides the ventrum from the dorsum and can extend to the outer surfaces of the limbs. On the lateral surfaces there is a black, middorsal mane which features long, silver hairs interspersed throughout. The sides of the limbs and neck range from buff to orange, while the upper surfaces of the hands and feet range from buff to grey. The proximal end of the dorsal surface of the tail is reddish-orange, gradually becoming black at the distal end. The ventral surface of the tail ranges from yellow to white (Hershkovitz, 1977; Walker, 1975; Wolfheim, 1983).

Both subspecies possess vibrissae that protrude laterally, the mastoicals, and anteriorly, interrhinals, though the latter are more sparse in cotton-top tamarins than Geoffroy's tamarin. Both species feature darkly pigmented external genitalia, the skin of which is corrugated, surrounded by patches of darkly pigmented glandular skin. The anal region is similarly circumscribed by a darkly pigmented skin patch (Hershkovitz, 1977).

The individual uniqueness of each animal's coat probably enables tamarins to determine the identity of one another. Further, the striking patterning of color in many species is conceivably disruptive to the search images of potential predators. This variability in coat coloration sometimes makes the precise identification of the taxonomic status of individual animals in the field difficult. The most reliable features distinguishing Geoffroy's tamarins from cotton-top tamarins include the differences in the pelage on the cranial and nuchal crests. The reddish nuchal hair of Geoffroy's tamarin is not found on the cotton-top tamarin, while Geoffroy's tamarin does not possess the mid-sagittal white plume from which the cotton-top tamarin derives its colloquial name (Hershkovitz, 1977). Despite these obvious subspecific differences, taxonomic uncertainty pervades the literature. For example, reports on the feeding ecology of Panamanian tamarins, (Dawson, 1978, 1979; Garber 1981, 1984a) persist in referring to their subjects as *Saguinus oedipus*, implying that they are referring to the cotton-top tamarin (*S. o. oedipus*) and not Geoffroy's tamarin (*S. o. geoffroyi*). This state of confusion ultimately affected the choice of treatment variables employed in this study, with four of them allegedly being recordings of wild cotton-top tamarins when in fact, they proved to be recordings of Geoffroy's tamarins.

The present taxonomic fluidity of Callitrichids might be partially resolved if more characters were employed in the classification of the genus. Snowdon, Hodun, Rosenberger, and Coimbra-Filho (1986) have proposed the use of specific features in the long calls of golden lion tamarins (*Leontopithicus rosalia*) as taxonomic characters. Presently, golden lion tamarins are classified within one genus, consisting of three subspecies: *L. r. rosalia*; *L. r. chrysopygus*; and *L. r. chrysomeles*. Of thirty characters measured, seventeen of them, including the duration and fundamental frequency of long calls showed significant, reliable variation across the subspecies.

Similar procedures should be applied to the *Saguinus oedipus* group. While Geoffroyi's tamarin the white-footed tamarin and the cotton-top tamarin are all visually distinctive, the degree of their relatedness is still uncertain. There is a legitimate question as to whether these three animals should retain their subspecific status relative to one another or whether they are sufficiently distinct to warrant reclassification. If the work on golden lion tamarins is indicative, there will be significant co-variation in vocal morphology and anatomical variability within the cotton-top species assemblage. Determining the degree of relatedness between species will become critical as the space available for the housing of endangered primates becomes increasingly limited. If animals are not closely related, then they most certainly should not be interbred, a problem that has arisen more than once in the management of zoo animal populations.

Ecology and Distribution

For the purposes of this study, cotton-top tamarins and Geoffroy's tamarins will be treated as sub-species of the cotton-top tamarin. It should be noted, however, that some researchers contend that these are completely different species (Moynihan, 1970).

Saguinus o. oedipus is found in a small area of Central America and in northwestern South America, from southeastern Costa Rica to portions of northern Colombia. The western limit of its range is found at approximately 83 degrees west longitude, just west of the Costa Rican border. The eastern limit of its range is found at approximately 74 degrees west longitude, along the Rio Caca Boliva, in Colombia (Hershkovitz, 1977). It has been observed as far North as 11 degrees north latitude and as far south as 4 degrees north latitude, near the Pacific coast of Colombia, along the west bank of the Rio Magdalena Cauca.

Limits of the range of *Saguinus oedipus* should be understood to include those of Geoffroy's tamarins as well as those of cotton-top tamarins a potentially confusing state of affairs if the two tamarin populations ultimately are determined to represent distinct species. The two forms do not presently exist sympatrically; cotton-top tamarins are almost exclusively found in Colombia while Geoffroy's tamarins are found primarily in Panama.

Some researchers promulgate the hypothesis that Geoffroy's tamarin has only recently invaded Panama through corridors of secondary forest that have expanded as a result of recent human agricultural activities. Evidence for an assumed historical allopatric association between the two subspecies is absent.

The Colombian range of cotton-top tamarins lies between the Rio Atrato on the west, the Rio Cauca on the south, and the lower Rio Magdalena on the east. Its few remaining habitats lie within the Colombian departments of Cordova Boulivar Sucre Atlantico, Antio Quia, and Choco. Geoffroy's tamarin is abundant in Panama, and in the Colombian department of Choco (Hershkovitz, 1977). Geoffroy's tamarins and cotton-top tamarins are the only tamarins found west of the Andes mountains (Wendt, 1979). Within this broad geographic area, both tamarins are found at all elevations between sea level and 1500 m above sea level.

Geoffrey's tamarin is considered locally abundant in Panama, while the cotton-top tamarin is considered highly endangered in Colombia. The status of other populations in Costa Rica and western Colombia is not known. Dawson (1978) estimated population densities for Geoffroy's tamarins that ranged from 20-30 animals/km² in the Canal Zone. Neyman (1978) estimated population densities for cotton-top tamarins that ranged from 3 to 18 animals/km² in northwestern Colombia.

The home range of Geoffroy's tamarins averages 26 hectares, with as much as a 13% overlap between home ranges of adjacent groups (Garber, 1984b). Here the term home range is defined as the composite area obtained by averaging the maximum daily distance traveled by an animal or group of animals during daily foraging and maintenance activities (Devore, 1965). This is distinguished from a core area or territory which is the area wherein most activities are concentrated and which is actively defended against intrusion by conspecifics (Sussman & Kinzey, 1984). Although tamarins monitor the perimeter of the home range on a daily basis, foraging activity is concentrated near the center of the territory (Terborgh, 1983). Moynihan (1970) recorded group sizes for Geoffrey's tamarin that ranged from two to nine animals (mean = 3.9, n = 43). Geoffroy's tamarins utilize on average 2.06 hectares daily and reach densities of 27 to 36 animals/km² (Dawson, 1979). Typically, animals can travel as much as 2.06 km (± 0.04 km) within a 12 hour period (Garber, 1984b).

In Colombia, cotton-top tamarins are described as highly territorial, though their territories are somewhat smaller than those of Geoffrey's tamarins (Neyman, 1978). The home ranges of cotton-top tamarins average 7.8 to 10 hectares, and can overlap as much as 30% with those of other tamarins (Dawson, 1979). Neyman (1978) reported that group size in cotton-top tamarins ranged from three to thirteen animals per group with home ranges varying from 7.8 to 10.8 hectares.

In cotton-top tamarins there are often smaller groups of transitory animals that travel between the territories of established groups. These transient groups range in size from 1 to 5 animals. Tamarins can utilize up to 56% of their home range on a daily basis, traveling within a range of 1.5 to 1.9 hectares daily (Neyman, 1978).

Each of the two populations demonstrates slightly different habitat preferences--differences that could have profound implications for the success or failure of conservation strategies in the wild. Geoffroy's tamarins prefer secondary growth and edge habitats, whereas cotton-top tamarins prefer mature rain forest. Considering the rate at which the rain forest is being destroyed, it is not surprising that Geoffrey's tamarin has fared better than the cotton-top tamarin.

Along the Pacific coast of Panama, Geoffroy's tamarins is located most commonly in areas with annual rainfall levels that range from 10.8 inches to 27 inches. In other parts of its range, rainfall can approach 68 inches per year, most of which occurs between April and December. During the four month-long dry season, as little as four inches of rain can fall, resulting in a loss of up to 40% of the vegetative cover. Temperatures throughout this range average 80° F.

Geoffroy's tamarins are often found along forest edges and in secondary scrub forest. Most commonly, this includes low, bushy secondary vegetation, tangles, and vines. They do not thrive in mature, humid rain forest habitats, apparently requiring earlier successional stages of vegetation than their Colombian counterparts (Moynihan, 1970; 1976). Often, these habitats features large evergreen shade trees (Dawson, 1979). Geoffroy's tamarins seem to prefer trees with broad, leafy crowns with heights averaging 14.0 m (± 5.0 meters). Dawson (1978) has also recorded the presence of Geoffrey's tamarin in secondary growth arising after agricultural fields have been abandoned. These fields are characterized by low brush and vine-covered edge vegetation interspersed with tall, non-deciduous trees.

In northern Colombia, cotton-top tamarins are found in mature rain forests and in some deciduous forests, including areas along forest fringes that feature secondary vegetation. Some authors report that the animals are found exclusively in dry, tropical rain forest and in low, secondary forests (Hershkovitz, 1977; Neyman, 1978). The cotton-top tamarin is found most frequently at heights within the canopy ranging between 2 and 18 m (Hershkovitz, 1977).

To varying degrees, all Callitrichids are vertical clingers and leapers. This terminology refers to the particular mode of arboreal locomotion observed in Callitrichids. All Callitrichids are light and can travel along extremely narrow terminal portions of branches where separate trees converge in the matrix of the canopy (Garber, Moya, & Malaga, 1983). Tamarins can spend up to 59% of their daily time budget traveling within the canopy, with up to 75% of lateral travel occurring on branches with diameters of approximately 10 cm (Garber, 1984b). Unlike many larger Cebids, tamarins seldom descend to the ground for lateral travel. There is a virtual layering of the canopy which imparts a greater complexity and niche diversity to the forest habitat than is outwardly apparent (Grand, 1984).

Tamarins sleep in the crevices formed by the intersection of branches with the trunks of trees. When preparing to retire for the evening, tamarins enter a state of torpor, probably to conserve energy and reduce heat loss. When nesting, tamarins huddle in groups that are visually reminiscent of termite mounds, probably providing some degree of camouflage against predators (Dawson, 1978; Ted Heffler, personal communication, 1986). The animals sleep in a curled position, the face in contact with the ventrum and the head placed between the forelimbs, probably to cover the head plumage, which, if visible, would reduce the level of crypsis. Cotton-top and Geoffroy's tamarins are more active than most other tamarins. During warm weather, the average foraging day length is 676 minutes (± 62 minutes). On humid or rainy days, foraging time falls to 426 minutes (Dawson, 1979). This finding implies that humidity exerts a dampening effect on the activity of at least some species of tamarins.

On average, only 14.2% of the activity budget of Geoffroy's tamarins is devoted to resting, whereas in the saddleback tamarin up to 42% of the activity budget is devoted to resting (Terborgh, 1983). In cotton-top tamarins, 23.4% of the time is spent in foraging and feeding, while 48.6% of the total activity budget is devoted to traveling (Neyman, 1978; 1980).

All Callitrichids are crepuscular, exhibiting feeding and activity peaks in the middle of each morning and afternoon (Garber & Easley, 1982). These intensive periods of foraging are separated by intervals of relative quiescence. When resting, the animals are often draped over branches with all four limbs hanging limply downward, indicating complete relaxation (Hampton, Hampton, & Landwehr, 1966). Of all of the tamarins, Geoffroy's tamarin arises later than any other. They begin to awake approximately 45 minutes after dawn--between 06:00 and 06:30 A. M. --and continue their activity until 30 minutes before dusk (Moynihan, 1970). Dawson (1979) records that in Geoffroy's tamarins, the first animal emerges from the nest approximately 11.7 minutes after sunrise, and that the last animal enters the nest 34.2 minutes prior to sunset. Similar values have been reported for the saddleback tamarin (Yoneda, 1984a). Cotton-top tamarins usually arise 30 minutes after sunrise and begin foraging within 4 minutes of leaving the nest (Neyman, 1978).

There is a precise ordering to the positioning of cotton-top tamarins within a group as they exit and enter their nest sites. In the morning, the adults are the first to emerge from the nest, followed by the youngest infants, the next oldest juveniles, and finally by the oldest offspring. In the evening, upon returning to the nest site, the adults again lead the procession, followed by their offspring in order of ascending age. This ordering possibly serves to reduce the probability of agonistic interactions by spatially and temporally separating isosexual animals of equivalent age (Wolters, 1978).

Feeding Ecology

Tamarins belong to the guild of diurnal, arboreal omnivores, and foraging is their predominant activity during the day. As much as 25 g of food per animal are consumed daily, yielding approximately 200 C/kg of body weight. Analysis of stomach contents suggests that 10% of food items consist of plant matter, 60% fruit, and 30% insect prey by weight (Dawson, 1979; Garber, 1984a). Leafy materials constitute up to 2.3% of the plant mass, seeds constitute 1.5%, and flowers comprise 0.1% of the mass.

Moynihan (1976) reports that 20% of the food mass in the stomachs of Geoffrey's tamarins consists of insect parts and 7.2% consists of cellulose. There is a morning peak in foraging which begins shortly after animals emerge from their nests, probably to replace food that has been digested during the night and another during the afternoon, probably in preparation for nesting. During the morning hours, torpid insects are primarily consumed. As the habitat becomes warmer, insect prey become increasingly active and plants become the primary source of food (Dawson, 1979; Hershkovitz, 1977).

Cotton-top tamarins consumes a variety of insects, fruits, flowers, nectars, and plant exudates. Leaves are seldom utilized as food sources, primarily due to their poor nutritional content. Food is consumed where it is found, not transported back to a nest. Water requirements are partially met by the consumption of dew that collects on leaves. It is lapped directly from the surface of the leaf or from small depressions on other plant surfaces.

Although there is some variation, most tamarins concentrate their foraging activities at heights ranging from 20 m to 25 m above the ground (Terbourgh, 1983). Most tamarins concentrate nearly 50% of their activities in trees with crown diameters smaller than 15 m in circumference. Trees with crowns of this diameter often exhibit sequential ripening of fruit, making ripe fruit with diameters of approximately 1.5 cm constantly available throughout the growing season (Dawson, 1979; Garber, 1984b).

Plant exudates also comprise a significant component in the diets of some Callitrichids, especially the pygmy marmoset and to a lesser extent cotton-top and geoffroy's tamarins (Garber, 1981; Neyman, 1978). Whereas pygmy marmosets are obligate exudate feeders obtaining exudates through tree gouging, tamarins consume exudates opportunistically, exploiting plants damaged by insects or other animals (Sussman & Kinzey, 1981). The plant species most often exploited for its exudate is *Anacardium excelsium*; Geoffroy's tamarins devoting 14% of its exudate feeding to this species and deriving 23% of all plant exudates from this source (Garber, 1984a; Garber & Easley, 1982). Tamarins exploiting plant exudates spend less time foraging and can survive in smaller, more defensible territories (Stevenson, 1986).

Plant exudates are rich in some proteins, minerals, and reducing sugars, including arabinose, galactose, and methyl pentose, making this a high energy, carbohydrate rich food source. Another feature of plant exudates is their high calcium to phosphorus ratio (142 to 1). This might counteract the high level of phosphorus found in insect carapaces, another important component of the Callitrichid diet (Dawson, 1979). The levels of calcium found in most fruits are relatively low and may not be sufficient to restore the calcium to phosphorus ratio that can be imbalanced when large amounts of insect prey are consumed. Calcium imbalances are implicated in poor skeletal development, impairing locomotor function. Hence, exudate feeding could function to counterbalance high rates of insectivory.

Geoffroy's tamarin appears to be slightly more insectivorous than other tamarins. This relatively high rate of insectivory results in a reduction in the total amount of time required for foraging. Up to 39.4% of the time spent foraging is devoted to the capture of insects, 38.4% is dedicated to the acquisition of fruit, and 13.4% of foraging time is devoted to exudate feeding (Garber, 1984a, 1984b). Analysis of stomach contents suggests that from 38% to 64% of the diet of Geoffroy's tamarins consists of insect prey, with 67% of the insect mass consisting of *Orthoptera*, *Hymenoptera*, and *Colioptera* (Dawson, 1979; Garber, 1984a; Sussman & Kinzey, 1984). The optimum size for an obligate insectivore is approximately 100 g, less than the typical weight of an adult tamarin, suggesting that tamarins function as facultative insectivores (Terbourgh, 1983). The relative contribution of each class of food to the diet of tamarins varies seasonally with changes in their relative abundance. The cotton-top tamarin exhibit some seasonality in its consumption of exudates, with a peak in February and March. The birth peak for Geoffroy's tamarins occurs between March and June, suggesting that the increased consumption of plant exudates serves to maintain calcium levels in lactating females (Garber, 1984a).

Menzel and Juno (1985) have determined that the spatial and temporal distribution of ripening fruit has influenced the foraging strategies and problem solving abilities of tamarins. The clumped distribution and sequential ripening of preferred fruits favors a constant, low level of foraging. Further, the animals demonstrate a relatively well developed object memory, recognizing discrete features in their surroundings for up to 24 hours after last seeing them. Tamarins must be able to recognize and remember the location of food, often from one foraging cycle to another. This type of foraging strategy has enabled many species of tamarin to thrive in extremely variable habitats.

Mating and Social Systems

Animals form groups to facilitate the defense of limited resources and to enlarge their sensoria to more efficiently detect predators (Krebs & Davies, 1987). Cooperative resource defense and antipredator behavior exert some influence on the kinds of social and mating systems found in primates (Tilson, 1986). Virtually all diurnal primates live in some kind of social group, probably as a defense against predation (Jolly, 1985; van Shaik, 1983). The presence of spatially or temporally heterogenous resources also favors the aggregation of primates (Kummer, 1971). Additionally, microhabitat preferences might operate to bring animals together into groups (Rowell, 1972). Habitats featuring resources rich in caloric content can support larger, more concentrated groups, while habitats featuring diffuse resources with relatively low caloric content support smaller, more diffuse groups (van Shaik, 1983). Typically, terrestrial primates live in larger groups than arboreal primates (Jolly, 1985; van Shaik, 1983).

Until recently, most research on primate social behavior has concentrated on polygynous, Old World species (Devore, 1965; Kummer, 1971). However, much contemporary research focuses on the biology and behavior of New World primates, many of which are monogamous (Evans, 1983a). This system is defined as one consisting of an exclusive, preferential association between a mated pair of adult animals. Monogamous animals are characterized by reduced or absent sexual dimorphism, delayed sexual maturation, reduced external evidence of estrus in females, minimal sexual solicitation by females, high intrasexual aggression, mutual care of infants, and an extended period of development (Tilson, 1986). Kleiman (1978) states that fewer than 3% of all mammalian species are monogamous, though slightly more than 30% of extant nonhuman primates can be classified as exhibiting some degree of monogamy (Mitchell & Maple, 1985).

Outwardly, the social systems of Callitrichids resemble those of other strictly monogamous primates, e.g. white-handed gibbons and titi monkeys (Garber, 1984b; Mason, 1965). However, recent research suggests that, with the exception of golden lion tamarins few Callitrichids are strictly monogamous (Garber, 1984b; Kleiman, 1985b). Monogamy is an adaptive mating system in habitats characterized by limited resource availability and can function as an isosexual spacing mechanism that limits the number of potentially available mates (Tilson, 1986).

Monogamy is also characterized by extensive bi-parental care of relatively few offspring, increasing their survival rate--and the inclusive fitness of the parents (Kleiman, 1985b; Sussman & Kinzey, 1984; Wolters, 1978). Prolonged association between parents and their offspring enables parenting skills to be imparted to young animals, increasing the probability of their future reproductive success (Goldizen & Terborgh, 1986). The roles of both sexes are similar, resulting in reduced sexual dimorphism. However, males tend to be more involved with territorial defense, while females are more involved with intragroup stability (Wolters, 1978).

Depending on the species, the mating systems of tamarins have been described as cooperative polyandry or facultative monogamy. For example, the mating system of saddleback tamarins resembles cooperative polyandry (Goldizen & Terborgh, 1986) while that of cotton-top tamarins resembles facultative monogamy (Snowdon, 1990). The social system of most tamarins resembles a paired dominance hierarchy, as exemplified by Geoffroy's tamarins (Garber, 1984), saddleback tamarins (Epple, 1978), and white footed tamarins (Hershkovitz, 1977).

The basic nuclear group consists of an unrelated pair of adults that form a relatively durable pair bond, older adolescents from earlier births, and the most recent offspring (Tilson, 1986). Each adult pair remains together for life or at least throughout several successive mating seasons.

The common marmoset provides the basic model for pair bond formation in Callitrichids (Evans & Poole, 1983). In newly introduced pairs of common marmosets, affiliative behavior, such as approaching, remaining close, touching, grooming and its solicitation, olfactory investigation, and sexual behavior show initially high rates which decline in frequency after 10 weeks. This implies that these behaviors are important in the formation of the pair bond in Callitrichids. Males are the primary instigators of these activities, displaying more affectional behavior than females. Neyman (1978) suggests that the solicitous behavior of males toward females implies that females are exercising choice based on the performance of the males, stimulating competition between them. Once a pair bond is established, however, females appear to be more attached to males than males are to females (Wolters, 1978).

The presence of a mated pair does not necessarily imply that other, unrelated adults do not share their home range. In cotton- top tamarins there are high numbers of animals which range freely between the occupied territories of mated pairs (Dawson, 1978; Neyman, 1978). Marking studies suggest that many of these floaters are subadult females and slightly older males which are the offspring of territory holders and have emigrated from their parents' core territories (Neyman, 1978). Emigration from the nuclear group might be encouraged by isosexual parental aggression toward the maturing young and is probably an important mechanism inhibiting inbreeding (Garber, 1984b).

Over time, the composition of groups changes through emigration and immigration, though the structure and stability of nuclear groups remains relatively constant (Dawson, 1978; Neyman, 1978); however, within the genus there is considerable variability in the structure of the nuclear group. For example, in mustache tamarins there can be more than one adult female, though only the dominant female is reproductively active (Box & Morris, 1980). In saddleback tamarins there can be two or more adult males, all of which mate with the female (Garber, Moya, & Malaga, 1984; Goldizen & Terborgh, 1986). This probably represents a form of cooperative polyandry as opposed to the more common facultative monogamy (Goldizen & Terborgh, 1986). Cooperative breeding systems might be adaptive if increased numbers of males result in more assistance with the rearing of infants, especially if this assistance allows the female to produce more than one set of twins each year. Uncertain parentage favors the involvement of each adult male in the care of the infants.

Other Callitrichids which do not appear to be strictly monogamous include common marmosets (Evans, 1983b) and mustache tamarins (Box & Morris, 1980). Both species exhibit high levels of emigration and immigration, and this is characteristic of cooperative breeding systems. The levels of emigration and immigration observed in Geoffroy's tamarins (Dawson, 1978) and cotton-top tamarins (Neyman, 1978) are relatively low, characteristic of monogamous mating systems. Troops of cotton-top tamarins are smaller than those of most other tamarins, often consisting of a single pair of adults and one pair of adolescents (Neyman, 1978). This small group size is probably a result of the limited amount of care that can be provided for the young by a single pair of animals (Tilson, 1986). In fact, the amount of infant care provided by each parent is largely determined by the presence of older siblings. When adolescent young are absent, both parents engage in approximately equivalent levels of care. If, however, there are older siblings present, the adult male performs more carrying than the female. The greater amount of male carrying persists even though infants demonstrate a preference for the female (Cleveland & Snowdon, 1984).

The number and age of offspring influences the types and levels of other behaviors in a group as well. If twins are present, there is more play than when there is only one infant. The presence of older siblings exerts less influence on the amount of play than the presence of larger numbers of juveniles of equivalent age.

As infants mature, the amount of time that the adult male and older siblings spend carrying them decreases. When they reach thirty days of age, they are capable of and begin to exhibit free locomoting and play behavior (Cleveland & Snowdon, 1984; Tardiff, 1986).

The small groups of cotton-top tamarins are not as effective as the larger groups typical of other Callitrichids at predator detection or resource procurement. Saddleback tamarin groups, for example, possess greater numbers of adult males, which can aid in the care of the young, detection of predators, and discovery of resources. Since group size is determined by the availability of resources, changes in their availability can alter the group size and social structure of many species (Lott, 1984). For example, groups of Geoffroy's tamarins become less stable and often disintegrate when resources become scarce during the dry season (Dawson, 1978). Competition for limited resources not only influences group structure but also governs interactions between individuals, sometimes leading to increased intraspecific aggression.

Social Relationships

Many traditional behavioral scientists operationally define dominance in terms of the number of aggressive displays, level of agonism, quantity of limited resources procured, and numbers of mates and matings secured. This traditional perspective under-emphasizes the complexity, contextual dependency, and dynamic quality of dominance (Mitchell & Maple, 1985). Important in a revised view of dominance is a de-emphasis of the concept that dominance is an inherent quality of individuals. The term suggests a relationship between at least two individuals which can change over time. Dominance involves an array of attributes related to social competence which is gradually acquired and expressed through ontogeny. Social experience correlates highly with social position; socially deprived animals seldom attain high positions in a hierarchy (Mitchell & Maple, 1985).

Dominance, as it relates to Callitrichids, is best viewed in terms of two parallel dominance systems (Epple, 1978; Garber, 1984b). Neither sex is necessarily dominant over the other, but dominance relationships do exist between isosexual individuals. Dominance relationships are maintained through aggression, most frequently between isosexual adults or between parents and their isosexual offspring. The absence of significant sexual dimorphism in monogamous species eliminates the size advantage that males possess over females in polygamous species. Consequently, the level and directionality of heterosexual aggression is reduced in Callitrichids (Tilson, 1986). For example, female Callitrichids are capable of defending resources against the depredations of males (Tardiff & Richter, 1981).

Young adult animals, less established in a hierarchy are subordinate to most older animals in the group. As individuals mature, they may advance in rank within the group. Conversely, as individuals senesce, they may lose their social position. For tamarins, as for all other primates, adolescence is a time of low social status and high levels of stress (Mitchell & Maple, 1985). Adult patterns emerge gradually, with much variability between individuals. Maturity is marked by a reduction in play behavior and an increase in aggressive and sexual interactions. This process continues until adulthood and then reverses after the individual has passed its prime.

Adult aggression toward adolescents probably encourages emigration from the natal group. This dispersal mechanism increases the distribution of specific genotypes across a broader range of environmental conditions (Evans, 1983a).

Immature Callitrichids remain with their parents for extended periods of time. Consequently, mechanisms have evolved to inhibit their reproduction and minimize the possibility of inbreeding. Parental aggression toward isosexual offspring could inhibit reproductive behavior by elevating the levels of cortical steroids (Stoskopf, 1983). Dominant, reproductive females probably maintain their status over subordinate females, both behaviorally and chemically, through scent marking (Snowdon, 1990). The scent glands of dominant females are thought to exude compounds implicated in the suppression of ovarian cyclicity in subordinate females (French, 1982; French, Abbott, & Snowdon, 1984), while the act of scent marking possibly provides a visual signal attesting to the status of the marking animal (Snowdon, 1990). Whether reproductive inhibition is hormonally or behaviorally mediated has yet to be resolved.

Social interactions are facilitated by a species specific repertoire of signals, involving several sensory modalities. Dominance, as expressed by aggressive displays, can be communicated to other animals by open-mouth gape threats, yawning, direct stares, confident gaits, chasing, displacing, failure to yield, tail position, scent marking, and mounting. Submissive behaviors are characterized by attempts to withdraw from an interaction and include gaze aversion, grimacing, crouching, yielding, presenting, screeching, and flight (Mitchell & Maple, 1985; Napier & Napier, 1985). While competition for limited resources, including mates, can encourage aggressive interactions, once animals have become paired, affiliative interactions associated with reproduction predominate.

Reproductive Physiology and Behavior of the Callitrichidae

The general model describing the reproductive physiology and behavior within the Callitrichidae is provided by the common marmoset (Epple, 1975; Evans, 1983a; Evans, 1983b). Within the taxon, however, there is considerable variability (Snowdon, 1990).

The treatment of Callitrichids as a unitary, homogenous group has led to errors in the management of Callitrichid colonies and poor reproductive performance in some groups, notably cotton-top tamarins and golden lion tamarins (Wolf, 1981). Recent research on these two species provides better examples for understanding the reproductive physiology and behavior of *Saguinus* species (Kleiman, 1978; Snowdon, 1990).

Male cotton-top tamarins become sexually mature at twenty four months of age, while females become sexually mature at eighteen months of age, though they do not engage in sexual behavior until they are somewhat older (Brand and Martin, 1983; Evans, 1983a; Snowdon, 1990). Sexual maturity in females is determined by the onset of attractivity, proceptivity, and receptivity. Additionally, both sexes exhibit increases in the rate of scent marking as they approach sexual maturity (Tardiff, 1983). Proceptive behaviors are those that increase the likelihood of copulation, influencing the attractivity of the female to the male, while receptivity refers to the motivational state of the female governing her acceptance of the male, and facilitating copulation (Baum, 1983). Unlike most other mammals, the expression of reproductive behavior is not restricted to narrow periovulatory periods in primates, making the assessment of reproductive state difficult, particularly in Callitrichids. Reproductive condition is usually assessed behaviorally or through hormonal assays. For example, there is more proceptive behavior during the follicular phase of the ovarian cycle than during the luteal phase (Baum, 1983).

Olfactory cues seem to play a role in the modulation of reproductive behavior in primates, especially in Callitrichids (Epple, 1976). Estradiol apparently stimulates the synthesis of compounds that function as olfactory signals, increasing the attractivity of the female to the male (Baum, 1983).

The small size and relative absence of sexual dimorphism in Callitrichids makes identification of individuals difficult, and often identification is possible only when the genitalia are visible. Testicles in adult males, when fully descended, attain diameters ranging from 3 to 15 mm. The development of darkly pigmented circumgenital glandular fields indicates sexual maturity. These glandular fields are larger in females than in males and can be used to determine the sex of animals, even in the field (Neyman, 1978). The relative age and parity of females can be determined by observing the morphology of their nipples. Multiparous females possess nipples which are longer than those of nulliparous or primiparous females, often attaining lengths of 5 mm (Neyman, 1978).

Several studies have shown that the ovarian cycle of subdominant female Callitrichids is inhibited by the presence of dominant females, probably mediated through the deposition of chemical compounds throughout the surrounding area. Subdominant females in the presence of a dominant female exhibit a dramatic reduction in the cyclical variation in levels of urinary estrone and estrogen and an increase in serum progesterone concentration resulting in acyclicity. Removal of subordinate females from the vicinity of dominant females results in a rapid increase in estrone and estradiol and the restoration of cyclicity (Snowdon, 1990). The rate of scent marking performed by subordinate females also declines in the presence of dominant females, returning to normal levels only when the animals are separated (French, 1982).

One mechanism implicated in the suppression of ovarian cyclicity in subordinate females involves the stress related inhibition of the release of gonadotropin releasing hormone by the hypothalamus in the presence of dominant females. There is an apparent relationship between dominance status, endocrine function, and fertility (French, 1982). This phenomenon has been observed in several Callitrichids, including *Callithrix jacchus* (Evans, 1983a; Evans & Poole, 1983b) *Leontopithecus rosalia* (Kleiman, 1978), and *Saguinus oedipus* (Snowdon, 1990).

Radioimminunoassays of the concentrations of urinary gonadotropins and urinary hormones, including estrogen and estradiol, provide a non-invasive method for monitoring the ovarian cycle and reproductive state in female Callitrichids (Brand & Martin, 1981; French, Abbott, & Snowdon, 1984). In newly paired Callitrichids, elevated levels of urinary estrogen are correlated with decreased latency to and increased frequencies of mounting, while elevated levels of urinary progesterone are correlated with increased latency to and decreased levels of mounting (Brand & Martin, 1981).

A more accurate indicator of reproductive state is provided by leukocyte alkaline phosphatase (LAP) activity, which is positively correlated with the changes in levels of serum estrogen and progestin that occur during the ovarian cycle. LAP activity also increases during pregnancy and offers a more reliable indicator of this condition than abdominal palpation (Hearn, 1982).

Cyclical variation in the levels of urinary estrogens in cotton-top tamarins suggests an average ovarian cycle length of 22 to 23 days with a peak in sexual activity occurring between 12 and 14 days into the cycle (Brand & Martin, 1981). Other research suggests that the ovarian cycle in cotton-top tamarins ranges from 14 days to 19 days (± 2.7 days) as determined by the post parturition LH surge (Zigler, Bridson, Snowdon, & Eman, 1987). When the female is in estrus, there is no pronounced increase in soliciting copulations from the male. Copulations can continue until a few days prior to parturition (Brand & Martin, 1981), and can resume approximately 19 days afterward, during a post-parturition LH surge (Ziegler, Bridson, Snowdon, & Eman, 1987). Unlike most Cercopithecines, there are no profound changes in the morphology of the external genitalia during peak receptivity. Consequently, behavioral indices are often employed to estimate the stage of the reproductive cycle. One week before peak estrus, male cotton-top tamarins exhibit peaks in scent marking, olfactory investigations, huddling, and allogrooming, all directed toward the female. During peak estrus, the female exhibits a precipitous decline in scent marking, with a peak in scent marking one week after the cessation of sexual behavior (French, Abbott, & Snowdon, 1984).

In both sexes of golden lion tamarins and cotton-top tamarins, there is a pronounced increase in tongue flicking immediately preceding copulation (Moynihan, 1970). Unfortunately, not all behavioral indices of reproductive state are completely reliable. For example, huddling, which often occurs pericoitally also occurs if an animal is ill or if the ambient temperature decreases below an optimal range.

Moynihan (1970) describes the following sequence in the copulatory behavior of Geoffroy's tamarins. The male approaches the female from the rear and begins an olfactory investigation of her anogenital area. Often, his eyes are tightly closed during this investigation. The male straddles the female and begins to olfactorily investigate her nape. Copulation assumes the typical mammalian dorsal-ventral configuration, with the male standing quadrupedally, legs flexed, over the female while performing multiple thrusts.

Intromission occurs for periods not exceeding thirty seconds, though there can be multiple intromissions. During particularly vigorous copulations, the male may appear to attempt to climb up the back of the female. The tail of the female, which may have been tightly coiled at the onset of coitus, may begin to uncoil as copulation proceeds. There are no overt signs of ejaculation, though some researchers report a prolonged terminal intromission with a quivering of the pelvic region in the male. Post copulatory behavior usually includes anogenital self-grooming or facial allogrooming by both animals (Moynihan, 1970).

The frequency of copulatory behavior is influenced by the degree of familiarity between two animals. When animals are first introduced, the frequency of copulation can approach once per hour, declining to one episode per day as the animals form stable, long-term pair bonds (Evans, 1983a).

Copulations are seldom observed in the wild and even less frequently in captivity (Kleiman, 1978). This being the case, and except for a slight amount of vaginal bleeding, the timing of ovulation being so difficult to determine that the inception of a pregnancy often proceeds undetected. Abdominal swelling is minimal until the pregnancy is well advanced, and is usually not confirmed before fourteen weeks of development (Kleiman, 1978).

Although abdominal swelling in nulliparous and primiparous animals is discernible, with each succeeding pregnancy the degree of swelling decreases, making assessment of the progress of pregnancies in multiparous animals difficult. Consequently, some managers of Callitrichid colonies attempt to determine the presence of a pregnancy by observing changes in behavior. In the common marmoset, increased appetite, increased water consumption, and increased sprawling are indicators of imminent parturition; although other researchers report that there are few changes in the behavior of females indicative of this condition (Epple, 1975; Kleiman, 1978). The mean length of gestation of the cotton-top tamarin is 183.7 days, with a range of 182.3 to 185.1 (Snowdon, 1990; Ziegler, Bridson, Snowdon, & Eman, 1987). This compares with a mean gestation period of 132 days for *Leontopithecus rosalia* and 144 days for *Callithrix jacchus*. In fact, the cotton-top tamarin has the longest gestation period of any Callitrichid, while the shortest gestation period has been reported in *Leontipithecus rosalia*, the largest of the Callitrichids (Kleiman, 1978). The median interbirth interval for cotton-top tamarins is 238 days with a range of 182 to 374 days according to Evans (1983a), although French (1983) suggests that the interval is closer to 208 days. The wide range of proposed interbirth intervals is probably an artifact of basing estimates on the degree of abdominal swelling. One striking difference in reproductive characteristics between Callitrichids is the high reproductive potential of *Callithrix* and *Cebuella spp.* compared to the much lower reproductive potential of *Leontopithecus* and *Saguinus spp.* (Evans & Poole, 1983; Evans & Poole, 1984). The two former genera can produce as many as 3 or 4 young per pregnancy while the latter genera produce only 1 or 2.

The influences of captivity on reproduction appear to be more deleterious in the latter two genera compared to the former two genera (Snowdon, Savage, & McConnell, 1985; Tardiff, Carson, Gangaware, 1986). For example, tamarins respond poorly to many captive rearing schemes, including hand rearing. Further, more infant tamarins are found suffering from injuries inflicted by inexperienced parents than are young of the two former genera (Hearn, 1975; Hampton, Hampton, & Landwehr, 1966). Consequently, it is imperative that animals be allowed to develop in adequate social environments, including those featuring parents and older siblings. Not only does this improve parenting skills, but it allows animals to develop a full repertoire of adult behaviors, including reproductive behavior (French, Abbott, & Snowdon, 1984).

Births are concentrated during January through April in the neotropics but are concentrated during March through August in the north temperate zones (Hearn, 1982). This shift in birth peak also occurs in other taxa of neotropical fauna when they are transposed to more northern, temperate latitudes (Johnston & Milton, 1984), suggesting that photoperiod is important in the modulation of reproductive cycles.

At birth, the ratio of males to females is almost equal. Twins are produced in 75% of births, single animals in 16%, while only 8.7% of births produce triplets. Infant tamarins can weigh as much as 30% of the total weight of the mother, ranging between 35 and 41 g, with no significant differences between the sexes (Brand, 1981; Evans, 1983a). Births usually occur at night, making intervention during emergencies by technicians difficult. Many neonatal animals are lost because a birth has occurred and gone undetected (Kilborn, Sehgal, Johnson, Beland, & Bronson, 1983). Newborn animals must vocalize immediately if the mother is to attend to them (Rothe, Wolters, & Hearn, 1978). Shortly after birth, there is a grasping reflex performed to facilitate climbing by the infant out of the vagina and onto the ventrum of the female. Tamarins are born fully furred, though the color of the pelage is darker than that of the adult. The dorsal surface is heavily furred, the ventrum is lightly furred, and the cranial plume is already visible. The eyes are open, although the infants do not appear to be able to focus on objects in their surroundings (Kirkwood, 1983).

In cotton-top tamarins, only 9% of newborn animals born to naive, primiparous females survive beyond one year of age. If the mothers are allowed to obtain some experience with other infants, then this level rises to 63% (Snowdon, Savage, & McConnell, 1985; Tardiff, Carson, & Gangware, 1986).

Under traditional management schemes, up to 32% of newborn cotton-top tamarins are stillborn and as many as 21% of the survivors die within a week after parturition. The parity of the female and the number of young produced at each parturition influence survival rates, with increasing parity corresponding to an improvement in reproductive success (Brand, 1981). Up to 69% of singleton animals are stillborn while only 26% of twins are stillborn. As many as 42% of the young produced by primiparous females are stillborn, declining to 23% for succeeding births. Up to 90% of animals that survive the first month of life are likely to survive beyond one year of age (Snowdon, Savage, & McConnell, 1985).

Nearly 75% of infant mortality is directly attributable to mutilation by inexperienced, primiparous females (Kirkwood, 1983). Included in the design of a successful breeding program for Callitrichids should be provisions for allowing the young to remain with the parents for at least one cycle of reproduction, allowing them to gain some experience with newborn animals (Brand, 1981; Snowdon, Savage, & McConnell, 1985). Animals allowed to remain with adults and their subsequent offspring possess better parenting skills, both for their own young and for rejected unrelated infants placed in their care under fostering regimens (Collier, Kaida, & Brody, 1981). The presence of conspecifics can provide adequate social environments, but this is only one aspect of captive habitats that needs to be considered in the design of breeding programs.

The physical environment exerts profound effects on the reproductive performance of captive primates. Environmental stability and adequate sensory stimulation appear to improve reproductive success in several species of Callitrichid, including cotton-top tamarins (Snowdon, Savage, & McConnell, 1985). Habitats should include properly positioned nest boxes, which allow the mother to retreat from the group with her newborn young. Properly designed nest boxes can prevent the infants from falling to the floor of the enclosure where they can become injured (Evans, 1983a). Providing a secluded area for the female to undergo parturition could also reduce maternal stress and minimize the probability of abnormal maternal responses to the newborn (Hearn, 1982).

While the newborn young stay with the mother for the first few days, within 4 days the father begins to carry the young, returning them to the mother for nursing (Cleveland & Snowdon, 1984). Between 4 weeks and 14 weeks, of age, the male performs most of the carrying, although beyond this age the female shows a slight increase in the frequency of carrying behavior. At 3 days of age, the infants begin to visually track objects in their surroundings. Newborn animals can produce vocalizations and at one week of age begin to respond to nearby sounds, including vocalizations of other tamarins. At one week, the caloric intake can exceed 200 to 300 C/kg per day, sometimes reaching 500 C/kg per day (Kirkwood & Underwood, 1984). This high energy requirement declines as the animals mature.

Cleveland and Snowdon (1984) report that at 12 days of age the weight has increased to 50 g. At this time the young can be removed from the parents and fed artificial infant formulas. At 2 weeks of age the infants can support themselves on their own limbs, and can perform foot behind ear scratching without losing their balance. At 30 weeks of age infants begin to exhibit play behavior. At 30 days of age infants weigh 30% as much as an adult and leave the backs of adults more frequently as they begin to perform locomotor and investigatory behaviors. Between 44 and 60 days of age, the animals begin to accept solid food (Herskovitz, 1977). At 6 weeks of age, more time is spent on perches and on the substrate of the enclosure, while less time is spent on the backs of adult animals. At 2 months of age, the average weight of the young has increased to 85 g (Cleveland & Snowdon, 1984).

Although the adult male assumes the role of primary carrier for the first 2 months of life, after 9 weeks this rate declines, and the role of carrier is increasingly assumed by younger males. After 10 weeks of age, the infants are seldom carried by the adult male. At this age, male infants show increasing amounts of rough and tumble play, usually with other young males but also with young females, which show very little isosexual rough and tumble play (Wolters, 1978). At 3 months of age, the average weight has increased to 181 g. At 14 weeks of age, the juvenile pelage is beginning to disappear and the adult coloration is beginning to develop. It is at this age that the animals are usually weaned (Kirkwood, 1983).

From 8 weeks to 20 weeks of age, the young animals interact with adults more than with subadult troop members. Play is the predominant social interaction between 7 months and 14 months of age, and is usually directed at younger siblings (Snowdon, Savage, & McConnell, 1985). Siblings beyond 14 months of age assist in carrying younger infants, while younger siblings are involved in initiating play with and transferring food to infants (Cleveland & Snowdon, 1984). This two stage developmental regimen in the acquisition of parenting skills could explain some of the failures of earlier attempts at hand-rearing cotton-top tamarins, one or the other component of experience often being omitted (Tardiff, Carson, & Gangaware, 1986; Tardiff, Richter, & Carson, 1984). At 2 years of age, the animals are nearly adults, but do not exhibit reproductive behavior until they are between 3 and 4 years old. The amount of interaction with other animals experienced by young tamarins influences their rates of development, age at independence, and future social competence (Tardiff, Richter, & Carson, 1984).

Inadequate knowledge of aspects of the biology and behavior of Callitrichids, including their social and mating systems has often resulted in ineffective strategies for maintaining them successfully in captivity. Because of their increasingly critical conservation status in the wild, strategies for improving their survival rate in captivity must be developed. In order to design more effective management strategies, a better knowledge of all aspects of their natural histories must be developed. An often overlooked aspect of the behavior of Callitrichids that might influence the success or failure of captive management strategies is their complex system of communication.

Social Communication in Nonhuman Primates

Social communication is the process by which the behavior of one individual changes the behavior or the probability of future behavior in at least one other individual (Altmann, 1967). Communicative acts consist of natural units of behavior, ranging from passive to active and are often highly ritualized.

The science of semiotics concerns the study of the underlying principles and structures of all communicative signals that constitute a code--an agreed upon transformation or set of unambiguous rules whereby messages are conveyed from one organism to another (Sebeok, 1977). Further, semiotics addresses the generation and encoding of messages, e.g., the propagation of signals in any sensorially appropriate form of physical energy for decoding and interpretation. Zoosemiotics is more narrowly concerned with signaling behavior within and between nonhuman species, while anthroposemiotics is concerned exclusively with communication between human beings.

In nature, zoosemiotic signaling is sometimes considered primarily affective, that is, emotionally mediated. Emotional states are often generalized rather than discrete, involving autonomic arousal in response to temporal exigencies. Signals that are autonomically mediated are less susceptible to voluntary control and appear to be less influenced by ontogenetic processes. Anthroposemiotic signals, in contrast, are characterized by greater degrees of voluntary mediation, detachment from pleasantness or unpleasantness, greater modification through learning and conscious decisions, and relative independence from autonomic influences (Sebeok, 1977).

Theoretical issues concerning the underlying causes of observable communicative behavior comprise a large component of the literature on communication. Broadly, the causes of this type of behavior are divided into internal (motivational) and external (environmental) factors, including external referents, especially the behavior of other animals (Smith, 1981; Zahavi, 1982). Additional issues concern the communicative significance of both observable and nonobservable behaviors.

Some early researchers attempted to define communication, especially vocal communication, exclusively in terms of an explicit correlation between acoustic dimensions and the underlying motivational state of the signaling organism. Contemporary researchers are more willing to embrace the concept that there is some cognitive mediation of the affective substratum (Scherer, 1985). As the behavioral complexity of increasing numbers of organisms is acknowledged, what were perceived as unsophisticated graded communication systems are increasingly viewed as more complex categorical systems featuring large signal repertoires. Properties of animal signals once thought to be exclusively human are now thought to include: increased semanticity or signal meaning; increased arbitrariness, that is, the quality of a signal's bearing little resemblance to its symbolic referent; and increased iconicity, the quality of a signal's covariance with some parameter of its symbolic referent (Marler, 1977).

Social communication specifically enables closely related animals to engage in cooperative behavior, facilitating increases in their inclusive fitness. Within local physiological races, through the evolution of dialects, it might foster speciation by inhibiting gene flow across dialectical boundaries between related sympatric species (Marler, 1977; Snowdon, 1985; Waser, 1985). Social communication can serve social groups by regulating intragroup and intergroup distances, maximizing the efficiency of resource utilization, and by facilitating the cooperative detection of potential predators.

Communication between organisms requires the production, emission, reception and perception of signals (Marler, 1977; Sebeok, 1977). Signals are conveyed through four primary channels, involving the visual, acoustic, olfactory, and tactile sensory modalities (Fobes & King, 1982). Communication can feature sequential or simultaneous signals conveyed through different modalities, complicating their study (Marler, 1977).

Each type of signal has physical attributes which can enhance or restrict its effectiveness under specific conditions. Visual signals, for example, allow for the transmission of complex, rapid real-time signals which require the expenditure of relatively little energy. However, they can only be used over short and medium distances when line of sight transmission is possible and are further restricted by photoperiodic considerations. Visual signals can provide exact cues about the identity and location of signalers.

Acoustic signals are more effective over long distances and can overcome line of sight and photoperiodic limitations, though with the expenditure of considerable amounts of energy, decreased locatability, and occasionally reduced information content.

Tactile signals are important in the reduction of aggression and maintenance of intragroup relationships but require extreme proximities between communicators, increasing the possibility of injury during agonistic interactions.

Olfactory signals are effective over long distances and persist in the absence of the signaler, but offer reduced information content and are difficult to modulate. Olfactory signals are important in individual recognition, assessment of emotional states, and reproductive interactions. Combinations of signal modalities may operate simultaneously, particularly when animals are close together--especially in social groups.

The habitat and ecological niche of an organism influence its sensory profile, dictating which sensory modalities are emphasized in its communication. For example, vision, the primary sensory modality in primates (Fobes and King, 1982), is emphasized over other modalities by species living in open habitats (Seyfarth & Chaney, 1984). Audition, the second most important sensory modality in primates (Rowell & Hinde, 1962), is emphasized over vision by species living in forest habitats, facilitating communication when visual signals are compromised (Marler, 1977). Animals which typically employ several modalities simultaneously tend to feature graded signal repertoires, while those emphasizing a single modality tend to feature more discrete repertoires (Marler, 1982). Species possessing sharply delineated, categorical repertoires include those inhabiting dense forests, e.g., virtually all New World primates, including Callitrichids (Moynihan, 1970; 1976). Discrete repertoires improve communicative efficiency in difficult habitats but also tend to limit the size of the signal repertoire. Conversely, graded repertoires appear more open and less stereotypic. Possibly, many graded repertoires are actually categorical, but current paradigmatic and technological limitations preclude the definition of their categorical delineations. In fact, even within discrete systems, there are increasing numbers of examples of variability both between and within categories (Cleveland & Snowdon, 1982; Green, 1975; Snowdon & Pola, 1978).

Signal variability appears to be greater in communication within social groups of familiar individuals than it is in communication between unrelated organisms, suggesting that signal variability within a taxon represents information content.

The physical form of signals has been influenced by the evolutionary history of species, the physical attributes of the habitats within which they evolved, and the unique ontogenies of individual animals (Ehret, 1980; Waser & Brown, 1986; Wiley & Richards, 1978). This is as true for communication in humans as it is for other species. The differences between communication in humans and nonhuman primates is probably a matter of degree, not of kind. Consequently, the acquisition of greater knowledge of communication systems in non-human primates could illuminate our understanding of the primordia of communication in our own species (Snowdon, 1982).

Visual Communication in Nonhuman Primates

Vision is the predominant sensory modality in primates (Fobes and King, 1982): Redican, 1975). Many primates possess anatomical features which enhance visual acuity, facial expressions, and postural displays. These specializations include large, forward facing eyes, completely enclosed in a bony orbit; overlapping visual fields, providing high degrees of binocularity; enhanced visual centricity, with a concomitant reduction in the width of the visual field; well developed foveal vision; a wide range of electromagnetic sensitivity, providing well developed color perception; and a reduction in the size of the muzzle, facilitating better frontal vision. The reduction in the size of the muzzle is accompanied by a reduction in the complexity of the vibrissae and a de-emphasis in their importance in signaling (Napier & Napier, 1985; Redican, 1975).

Anatomical features important in visual communication include strong countershading, strikingly colored facial masks, elaborate toupees or manes, and strikingly colored skin patches in the anogenital region (Napier & Napier, 1985; Walker, 1975). The highly specialized pelage of some primates, e.g., the cranial plumage of cotton-top tamarins, is thought to be a specialization that augments visual signals employing piloerection (Moynihan, 1976). Another class of visual cues involves stereotypic facial expressions, ritualized postures, and species specific locomotor behaviors.

There is a positive correlation between the physical size of a primate and the complexity of its repertoire of facial expressions, with smaller species exhibiting more stereotypic repertoires. Complicated facial expressions involving the eyes, eyelids, eyebrows, scalp, ears, and specialized patches of hair have been observed in most primates (Redican, 1975). Visual signals important in aggressive interactions are highly ritualized, probably to enhance communicative accuracy, reducing the probability of potentially injurious physical interactions. For example, the scalp can be retracted to expose the eyelids while the ears are simultaneously retracted, emphasizing the distension of the face in an almost universal expression of arousal amongst primates.

Threats in primates are often accompanied by open-mouth gaping, characterized by a widely open mouth, exposed canines, and visual fixation on the target object. Moynihan (1976) contends that the ubiquitous gaping observed in primates is a manifestation of defensive threat and is seldom followed by attack. Visual fixation appears to be a mechanism for directing social signals toward an opponent, increasing the probability of an interaction (Moynihan, 1970). Conversely, redirecting the gaze away from an opponent can terminate interactions (Altmann, 1967; Moynihan, 1970).

Individuals which are the targets of threatening stares often redirect their attention to other animals, often initiating a cascade of threats. This redistribution of arousal mitigates the probability of agonistic interactions within the group. Cascade effects are heightened in captive settings, where the ability of individuals to regulate spacing is often limited (Rowell, 1972).

Callitrichids possess the typical suite of primate characteristics associated with highly developed vision. All Callitrichids are capable of 90 degrees of lateral head rotation in either direction, providing a 180 degree field of rotation in the horizontal plane. While the relevant research has not been conducted on most tamarins, studies of vision in the related pygmy marmoset might be applicable to them. The interocular distance in pygmy marmosets is 13 mm, probably somewhat less than in most tamarins. The threshold disparity angle is 33.02 cm, roughly equivalent to the value observed in humans and correlative of well-developed binocularity and depth perception. This is a critical adaptation for an arboreal animal that locomotes through vertical clinging and leaping (Buchli, 1978). Savage, Dronzek, and Snowdon, (1983), have determined that cotton-top tamarins possess dichromatic color vision, probably similar to that of squirrel monkeys, though the degree of insensitivity to longer wavelengths of light in these and other tamarins has not yet been determined. Compared to most other anthropoid Primates, Callitrichids are considered limited in their ability to utilize facial expressions (Redican, 1975). Moynihan (1976) has described many of them as being "poker faced." Nonetheless, Callitrichids do employ facial expressions, including lip and tongue protrusion, brow lowering, forehead wrinkling, and ear flattening.

The mouth can be employed in a variety of signals. A slightly opened mouth can indicate that a vocalization has been emitted or that an attack is imminent. The degree of opening can impart information about the type of vocalization that has been emitted. Open mouth gape threats are employed during aggressive interactions. In Geoffroy's tamarins, these feature a widely open mouth, exposed canines, and visual fixation with completely exposed irises (Moynihan, 1970).

Lip smacking is observed in all tamarins, but--unlike the same behavior in Cercopithecines--indicates agitation, not affiliation. Similarly, lip protrusion indicates arousal, and is often observed post-coitally (Moynihan, 1970).

Tongue flicking is another visual signal involving the mouth. Rhythmic protrusions of the tongue are often associated with reproductive behavior, often performed by males investigating the anogenital regions of females, or by either sex pericoitally. Tongue flicking could represent sexual solicitation or a willingness to engage in other affiliative behaviors (Epple, 1975). It has also been observed during olfactory investigations of novel objects and unfamiliar tamarins. Conceivably, tongue flicking is associated with the chemical assessment of objects through the vomeronasal organ (Epple, 1975).

The eyebrows are often employed in visual signaling. Raising them results in an apparent increase in the size of the eyes. Eyebrow lowering is exclusively hostile, often accompanied by frowning, lip protrusion, and partial closure of the eyes, all of which represent aggressive or defensive threat (Epple, 1975).

The ears of Callitrichids are also important in visual communication. Most Callitrichids flatten their ears preceding or during hostile interactions, probably to reduce the possibility of injury to the pinnae during hostile interactions. Oddly, Epple (1975) reports that Geoffroy's tamarins do not flatten their ears during agonistic interactions. When ear flattening is accompanied by the slight retraction of the corners of the mouth, partially exposing incisors or canines, tamarins are displaying fearfulness or submission (Moynihan, 1970).

The tail of Callitrichids is also important in signaling. Moynihan (1970) describes the tail of tamarins as their most expressive appendage. Though it is not prehensile, the tail is highly muscularized. When running, tamarins often elongate their tails horizontally behind them or recurve them over their backs. The communicative significance of these positions is not presently understood. When tamarins are at rest, the tail is usually allowed to hang limply from the resting perch. If the tail is hanging vertically but is not relaxed, the animal is thought to be indicating moderate arousal. Twitching of the tail is indicative of a relatively high level of arousal, just as it is in felids (Moynihan, 1970). A tamarin that is preparing to rest or sleep will often bring its tail forward and place it between its legs or will coil it around its feet or body as it sits on a resting perch, either to reduce heat loss or visibility to potential predators (Moynihan, 1976).

Tail coiling can be indicative of proceptivity in female tamarins or submission in juvenile animals. In Geoffroy's tamarins, the upward coiling of the tail is exclusively precopulatory in nature (Moynihan, 1970).

Another group of displays involves postural adjustments. For example, an aggressive stance is characterized by an erect posture or half crouch. When crouching, the forelimbs are firmly planted, the head faces forward--with eyes fixed on the target, and the body sways sinuously from side to side. This posture, or its bipedal variant, is often a prelude to attack (Moynihan, 1970).

Piloerection is a ubiquitous visual signal in many mammals, including Callitrichids. The communicative significance of piloerection is that it increases the apparent size of signalers to potential adversaries and competitors. Piloerection is exclusively associated with elevated levels of arousal. Piloerection of the crown or tail often occurs when animals attempt to approach, retreat from, or engage in agonistic encounters with other tamarins.

Moynihan (1970) suggests that, in Geoffroy's tamarins, the level of arousal can be assessed by observing the proportion of the tail that is piloerected. The greater the length of the tail with piloerected hair, the higher the level of arousal.

In addition to specialized coloration on their coats, all Callitrichids feature some degree of countershading. Moynihan (1970) suggests that the strongly countershaded white ventrums of most Callitrichids function to startle potential adversaries when they are suddenly displayed juxtaposed to the normal cryptic coloration of the dorsum. This imposition of white fields over cryptic background colors is probably similar to the mechanism underlying the exposure of teeth in certain displays. In each instance, the extreme visibility and controllability of white attributes provides a directable source of modulatable signals.

Despite the emphasis on vision in the *Anthropoidea*, there are some groups within the infraorder, e.g., Callitrichids, that emphasize other sensory modalities, including olfaction.

Olfactory Communication in Nonhuman Primates

While most terrestrial mammals are considered "macrosmatic," suggesting that olfaction is one of their primary sensory modalities, primates are considered "microsmatic," implying that other sensory modalities are emphasized over olfaction; there is a reduction in the mass of the olfactory bulb compared to that of the remainder of the central nervous system. This trend is evident even in Prosimians and Callitrichids, two groups for which olfaction remains an important sensory modality (Epple, 1975; 1985). The retention of a well developed olfactory system could represent an adaptation for communication within dense forest habitats, wherein visual signals are compromised.

Olfaction has, until recently, not been well examined in primates. This situation could be a result of the traditional emphasis by primatologists on the study of Old World anthropoids, a group in which olfaction plays a secondary role in communication, or it could represent an anthropocentric perspective on the relative importance of olfaction compared to other sensory modalities (Moynihan, 1970). The importance of chemical communication to Callitrichids is suggested by the retention of a functional vomeronasal organ (Epple, 1985).

Olfaction can provide a means for an animal to assess the species, sex, age, social status, reproductive condition, emotional state, and individual identity of other animals. It has also been implicated in the maintenance of territories, regulation of group integrity, maintenance of social dominance hierarchies, reduction in intra-group tension, establishment of pair bonds, and influencing the interactions between parents and their offspring (Epple, 1976; Epple & Smith, 1985). Olfactory signals can provide a means for establishing, delineating, and maintaining territorial boundaries and commonly traveled routes within home ranges because they persist in the habitat in the absence of the signaler.

In Callitrichids, chemical signals are implicated in the inhibition of the ovarian cycle in sub-dominant females by dominant females (Epple, 1985). The urine and vaginal secretions of females contain estrogens and short chain aliphatic acids, which can provide males with chemical cues that allow them to assess a female's reproductive state, inhibit the ovarian cycle in subdominant females, synchronize the ovarian cycles of nearby females, encourage the formation and maintenance of pair bonds, and facilitate the precise identification of mates.

Olfactory signatures can be specific to an individual, troop, deme, or species. Olfaction is important in the specific identity of individual animals, each of which possesses a unique chemical signature. Chemical signatures are derived from the sum of all metabolic processes and from sources in the specific habitat. Epple (1985) discusses chemical signals in terms of passive and active components. Sources of passive components include vaginal discharges, mucous, saliva, urine, feces, inadvertently acquired plant exudates, the products of their degradation by bacteria, and other chemical residues endemic in specific habitats--all of which can impregnate the pelage of animals.

Sources of active or emotive components include saliva, the secretions of apocrine and sebaceous glands, and excreted metabolic products in urine and feces. There is some overlap between these two broad classes of chemical signals.

Active chemical signals are almost exclusively glandular and associated with specific behaviors, especially scent marking. They are usually performed within the contexts of hierarchical interactions, agonism, reproduction, stress, frustration, fear, or alarm (Epple, 1985).

Virtually all Callitrichids demonstrate an interest in, and perform olfactory investigations of, the scent marks, secretions, and excretions of conspecifics. Olfactory investigations, in the form of social sniffing, are directed toward the muzzle and anogenital areas of target animals. Social sniffing involves the positioning of the muzzle of one animal at a distance of less than one cm from some portion of the body of target animals for extended periods of time. Anogenital sniffing, for example, has been observed in nearly all primates (Kummer, 1971), including the genital sniffing of infants by mothers (Devore, 1965). In some species, males perform olfactory investigations more than females, while in others olfactory investigations are performed equally often by both sexes.

Olfaction and scent marking in several Callitrichids, including the common marmoset and the saddleback tamarin have been the focus of several comprehensive studies (Epple, 1975; 1976; 1978; 1985). In the common marmoset, which often serves as a model for the biology and behavior of other Callitrichids, olfaction appears to be critical in the formation and maintenance of the pair bond. When individual common marmosets, or, for that matter, cotton-top tamarins, are first introduced to one another, there is an initially high rate of scent marking and olfactory investigation. However, as a pair bond matures, the rate of olfactory investigation and scent marking declines (Evans, 1983 b; Evans and Poole, 1983; 1984). In an established family group of cotton-top tamarins, scent marking persists at a relatively low basal level except during intertroop agonism or when strange animals are present, when it increases (French & Cleveland, 1984; Snowdon, 1990).

Scent marking involves the deposition of glandular products onto target surfaces in the immediate habitat. All Callitrichids possess apocrine or sebaceous glands concentrated in well developed fields in the sternal, superpubic, circumgenital, and circumanal regions (Epple, 1975; 1976; Sutcliffe & Poole, 1978).

Additional glandular tissue is located on the volar surfaces of the hands, feet, and ventral surface of the tail. The size and morphology of glandular fields is influenced by the sex, age, and social status of an animal.

In the adult common marmoset, the superpubic glandular field is located anterior to the genital region, the circumgenital glandular field circumscribes the genitals, and the sternal glandular field is located near the ventral thorax.

In adult male common marmosets, the most well developed glandular field is the circumgenital field, located on the anterior surface of the scrotum, extending to the perineum, and terminating in an annular patch on the posterior surface of the scrotum. The color of the circumgenital patch is grey to yellow in color, indicating the presence of both apocrine and sebaceous glandular tissue. These colors become more intense toward the posterior of the scrotum due to an increase in the density of nodules.

In adult female common marmosets, the most well developed glandular field is the circumgenital field, located on the labia pudendum. This field appears on slightly thickened skin, forming circum-vaginal pads that extend laterally and caudally from the vagina. The skin of the circumpubic glandular field is darkly pigmented and heavily impregnated with oily secretions. In the circumgenital region, the apocrine coils are larger than the sebaceous coils, while in the superpubic region, the sebaceous coils are larger than the apocrine coils.

The glandular skin is stippled with slightly elevated hair follicles, with an average interfollicular distance of 1 mm. Each macroscopically visible yellowish-white nodule represents a single, hypertrophied sebaceous gland. The apocrine glands empty into common atria of associated sebaceous glands, and both empty into piliary canals, often forming a common follicular cistern.

Sternal glandular fields are located in the integument of the sternoclavicular articulation region and are primarily composed of apocrine glands, which are more diffusely distributed than they are in either the superpubic or circumgenital regions.

In common marmosets, the glandular fields of sub-dominant males, subadult males, and females appear to be less well developed than those of dominant adult males. For example, the sternal glandular fields of dominant adult male common marmosets can attain diameters of 1.5 cm (Sutcliffe & Poole, 1978). However, the pubic regions of adult female cotton-top tamarins appear to feature slightly larger scent glands and glandular fields than those of adult males, averaging 4.56 cm^2 in females compared to 2.56 cm^2 in adult males. The anogenital glandular fields are also larger in females, averaging 3.43 cm^2, while those of adult males average 2.43 cm^2 (Neyman, 1978). The thickness of the glandular pads is greater in females than in males, averaging 1.46 mm in females, compared to 0.4 mm in males (Cleveland & Snowdon, 1984).

Most scent marking behavior involves the deposition of chemical signals, in the form of glandular secretions from the anogenital, superpubic, and sternal glands onto substrates in the animal's surroundings. The scent marks of common marmosets can be comprised of up to 96% of any of 15 esters of N-butyric acid, traces of squalene, and to a lesser extent, other glycoproteins (Sutcliffe & Poole, 1978). Additionally, although not well studied, mucous and saliva are sometimes deposited on substrates, and, conceivably, also contain chemical signals (Sutcliffe & Poole, 1978).

Scent is deposited on substrates by means of several specific postures and locomotor behaviors. The least frequently observed mode of scent deposition is sternal marking, most often performed by dominant adult male Callitrichids. Sternal marking involves pulling the body forward along a perch with the forelimbs or rubbing the ventrum laterally across a substrate while thrusting the thorax up and over the target surface (Moynihan, 1970). Sternal scent marking increases pericoitally or when animals are highly aroused.

Tamarins often perform anogenital or superpubic scent marking while straddling branches by lying on their ventrum, pressing the thoracic and abdominal surfaces against the substrate, and pushing themselves with their hind limbs or pulling themselves with their forelimbs, producing a slow anterior progression along the branch (Moynihan, 1970).

Sit rubbing is a particular type of anogenital marking which involves the lateral movement of the anogenital region over the target surface while the animal pulls itself forward with its forelimbs. Sit rubbing could also provide a means for depositing chemicals contained in urine or feces, or could function as a type of anal grooming (Epple, 1985). When some female Callitrichids perform sit rubbing, they exhibit clitoral erections. The erected clitoris and lip of the vulva can be deflected during sit rubbing, exposing the internal epithelium of the vagina and, probably facilitating deposition of secretory products.

Another type of scent deposition is superpubic scent marking, which is intimately associated with anogenital scent marking, involving the glandular field that extends anteriorly from the labia pudendum in females and from the anterior surface of the scrotum in males.

There are other behaviors that probably represent specialized forms of scent marking. For example, female Geoffroy's tamarins in estrus sometimes impregnate their tails with urine and other volatile compounds by pulling them forward between their legs. Males respond by taking the tails into their hands and investigating them olfactorily.

Virtually any surface within the habitats of tamarins can serve as a substrate for scent deposition. The most frequently marked substrates include distinctive protuberances, wooden perches, shelves, nest boxes, and any surface previously marked by another tamarin (Epple, 1985). Golden lion tamarins will deposit scent on wooden branches, nest boxes, pipes, windows, walls, and any distinctly protruding surface within their enclosures. Up to 64% of scent marking occurs near feeding sites, while only 20% occurs in situations devoid of food (Kleiman, 1978). Free living black-mantled tamarins regularly mark over the older scent marks of other troop members as they advance along branches during foraging (Izawa, 1978).

Scent marking is rare in very young Callitrichids. At birth, it is seldom observed, and when it does occur, there are no observable sex differences in the rates of marking behavior. In the common marmoset, there is evidence that scent glands are functional in five day old infants, though no marking behavior is observed (Sutcliff & Poole, 1978). As Callitrichids mature, especially during the first 20 weeks of development, rates of all types of scent marking, muzzle rubbing, defecation, and urination increase (Cleveland & Snowdon, 1984). For example, in cotton-top tamarins and Geoffroy's tamarins, superpubic and anogenital scent marking are not observed until nearly 20 weeks of age. In both species, at 30 weeks of age, glandular fields begin to exhibit a persistent precipitate and sternal scent marking begins to occur (Moynihan, 1970; Sutcliff & Poole, 1978).

As animals mature, sex differences in scent marking and urination rates begin to emerge. At two years of age, the microscopic morphology of the glandular tissue begins to become distinctly different in males and females. At this age, the animals are performing scent marking at essentially adult levels, with males performing sternal marking more frequently than females (Sutcliffe and Poole, 1978).

Dominant animals of all species and both sexes scent mark more frequently than subordinate animals, and sexually mature animals mark at higher rates than immature animals (Hampton, Hampton, & Landwehr, 1966). Scent marking involving the circumgenital and circumpubic glands is the most frequently observed in Callitrichids. The frequency of scent marking is correlated with levels of arousal, usually occurring at constant, low levels but increasing when animals are aroused (French and Cleveland, 1984). In most Callitrichids, females mark more frequently than males, up to 10 times as frequently in common marmosets. Sex differences are especially apparent in the relative rates of anogenital scent marking, though to a lesser extent, also apparent in the relative rates of super-pubic scent marking. There is little sexual dimorphism in the rates of scent marking involving the muzzle, feces, or urine. Unfortunately, female Callitrichids often urinate when performing anogenital scent marking, potentially confounding the data on dimorphic marking behavior (Sutcliff and Poole, 1978). Adult female cotton-top tamarins perform anogenital marking at the rate of 4.9 (±2.6) times per hour. Compared to other Callitrichids, this is an extremely high rate of marking, and is much higher than the frequency of marking performed by adult males. However, at two years of age, male cotton-top tamarins urinate significantly more frequently than females, a behavior which might serve as an alternative mechanism for the deposition of chemical signals.

The degree of sexual dimorphism in marking is less extreme in the saddleback tamarin (Epple, 1975), still less in common marmosets (Sutcliffe & Poole, 1978) and least in golden lion tamarins, where the sexes mark at nearly equivalent rates (Kleiman, 1978).

Within all Callitrichids, the frequency of scent marking increases when animals become agitated, immediately preceding defecation, when males are sexually aroused, or in response to changes in their immediate surroundings (Epple, 1975). In cotton-top tamarins, the rates of all categories of scent marking increase in response to the sounds of other tamarins, especially the territorial loud calls of conspecifics from unfamiliar neighboring troops (Cleveland & Snowdon, 1982; Kleiman, 1978). However, the rate of scent marking declines precipitously if animals become frightened.

The frequency of scent marking is profoundly influenced by the captive environment. Scent marking probably occurs at greater rates in zoos and laboratories because of the presence of other potentially dangerous or competitive animals, especially conspecifics (Epple, 1975).

Saddleback tamarins preferentially investigate the scent marks of conspecifics over those of congeners and the marks of dominant animals over those of subordinates (Epple & Smith, 1985). Male tamarins prefer the scent marks of females over those of males, while females prefer the scent marks of males over those of females. The scent marks of stressed animals are investigated more frequently than those of nonstressed animals (Epple, Alveario, & Katz, 1982; Epple, 1985).

Saddleback tamarins prefer recently deposited scent marks over older scent marks. One day old scent marks are investigated significantly more frequently than those that are two days old. Tamarins allowed to select enclosures containing scent marks deposited at different times will usually select the enclosure with the most recently deposited scent marks.

Many of the components of the glandular secretions of Callitrichids are of medium volatility and subject to accelerated degradation under conditions of extreme temperature or humidity. Nonetheless, saddleback tamarins can assess the identity of individual animals through scent marks that are 24 hours old, and animals continue to show interest in marks that are up to three days old (Epple & Smith, 1985).

These findings suggest that the rates of scent marking and other behaviors associated with territorial demarcation might be influenced by the proximity of other animals, especially conspecifics. To the extent that olfactory communication between animals induces stress or inhibits reproduction, it is an important aspect of the biotic environments of captive Callitrichids and requires more careful consideration. Unfortunately, its importance is often overlooked by managers of colonies of captive Callitrichids, who, in an attempt to maintain the cleanliness of enclosures, often disrupt this channel of communication through excessive cleaning (Hediger, 1950/1964), a practice which should be reexamined in light of recent information about the importance of chemical communication in Callitrichids.

While olfactory signals can function at great distances, another important mode of social communication, tactile communication, functions only when animals are in physical contact with one another.

Tactile Communication in Nonhuman Primates

Among the most ubiquitous of all communicative behaviors observed in primates is social grooming (Sparks, 1969; Altmann, 1967). Some researchers maintain that the primitive function of grooming was exclusively hygienic, and only secondarily functioned in social interactions (Altmann, 1967). Others suggest that this position is untenable, maintaining that in order for social grooming to have evolved, aggressive tendencies in the participants required tempering to allow even the most rudimentary grooming. The requirement that two potentially dangerous individuals assume extremely close proximities to one another in order to engage in grooming suggests that the hygienic and social functions of grooming must have evolved simultaneously (Hutchins & Barash, 1976).

Ultimately, social grooming functions to establish and maintain social relationships between familiar individuals, either as mates or as members of social groups (Sparks, 1969; Moynihan, 1969). Social grooming requires close proximities and physical contact between at least two individuals, requiring the inhibition of aggressive tendencies through the strengthening of affiliative relationships.

Social functions notwithstanding, grooming probably has important ramifications for the maintenance of the integuments of the individuals being groomed (Moynihan, 1969). Grooming removes sloughing epidermal flakes, hair, ectoparasites, and stray plant matter which may have become entangled in the pelage during foraging.

Allogrooming, the grooming of one individual by another, is preferentially performed on parts of the body that are difficult for animals to reach during autogrooming. This suggests that there is some hygienic function to allogrooming beyond its proposed social functions. Further, the animal performing the allogrooming might derive a slight but important nutritional benefit from food obtained through this activity (Hutchins & Barash, 1976).

Grooming can be performed with the digits, the tongue, or with the upper incisors, sometimes termed mandibular tooth combs. When allogrooming is performed, the claws are drawn through the pelage against the direction of the nap of the hair. The same procedure is observed during autogrooming, often accompanied by the frequent insertion of the digits into the ears and mouth. After an extended bout of either type of grooming, the claws are frequently visually inspected (Moynihan, 1969).

The directionality of dyadic grooming interactions is usually indicative of social status, with dominant animals most often being the recipients of grooming. Hence, especially in cercopithecines, dominant males receive the greatest amount of grooming from subordinate animals and females (Kummer, 1971). In some Callitrichids however, the directionality is reversed. Except during estrus, adult females typically allogroom dominant adult males more than they are groomed in return. In virtually all primates, males groom estrous females significantly more frequently than anestrous females (Devore, 1965; Moynihan, 1970).

In arboreal primates, and those that sleep together in common nests, the importance of social grooming in the reduction of intragroup tension is mitigated. Consequently, allogrooming occurs less frequently in many of these species, including most Callitrichids (Moynihan, 1969). In most primates, however, grooming is important in the moderation of group tension and frequently occurs after agonistic interactions. Conceivably, social grooming performed immediately following intense interactions functions to reestablish disrupted social relationships.

Grooming also functions as a type of displacement activity in aroused animals, and as such, appears to be undirected and contextually inappropriate. As with other displacement behaviors, grooming probably functions to dissipate excess energy (Tinbergen, 1952).

In most instances, grooming appears to be a pleasurable experience for both the animal performing it and for the recipient. The association of allogrooming with positive experiences probably facilitates durable, amicable physical interactions and enhances its function in maintaining social stability.

There are other tactile interactions that are distinct from but sometimes associated with grooming. For example, some researchers classify mounting as a type of tactile behavior (Devore, 1965). Its role in reproduction notwithstanding, mounting also functions to establish and maintain positions within social hierarchies. Dominant animals frequently mount subordinates, often regardless of the sex or reproductive state of the animal being mounted. While male mounting of estrous females is universal, homosexual mounting is frequent in many species, usually functioning as a mechanism for asserting social position.

Head grasping and wrestling are classified as tactile behaviors by some researchers (Moynihan, 1970). These interactions are frequently agonistic when they occur between adult males, though when they occur between adolescents, they appear to be exclusively affiliative.

Muzzle rubbing, important in scent deposition, is also thought to function as a type of affiliative tactile behavior. Muzzle rubbing is frequently observed between mated adults in several species of tamarins (Moynihan, 1970).

Finally, huddling and tail twining are usually treated as affiliative tactile behaviors (Kummer, 1971; Moynihan, 1970; Robinson, 1979). Both behaviors occur frequently in monogamous primates, including Geoffroy's tamarins and titi monkeys, functioning in the establishment and maintenance of pair bonds (Moynihan, 1970; Robinson, 1979).

Tactile communication provides a means by which the integrity of social groups can be regulated at close range. Obviously, this is only possible when animals dwell together in adequate social environments, a requirement that has not always been achieved in captivity. Fortunately, primates are increasingly maintained in social groups reminiscent of those formed by free living conspecifics.

Where animals are not in close contact with one another, the auditory sensory modality can facilitate communication over considerable distances through vocal signaling.

Vocal Communication in Nonhuman Primates

The current interest in the vocal behavior of nonhuman primates is partially predicated on the assumption that the study of primate vocal signaling will illuminate the evolutionary origins of human speech. The term "speech," while reserved exclusively to describe human vocal signaling, is considered by some researchers to be homologous to some of the prelinguistic vocal signaling observed in other primates, the study of which could offer models that adequately describe the probable origins and evolution of speech in the hominid ancestor (Lieberman, 1977).

It is clear that language can exist in the absence of speech, and that some nonhuman primates possess sufficiently complex neural substrates to effect complex vocal communication. Some species--especially those exhibiting neural lateralization--possess neural structures which could be homologs of structures found in humans and which are important in vocal communication. The study of the auditory and vocal behavior and its underlying neural mechanisms in nonhuman primates might not only establish plausible evolutionary sequences in the evolution of human speech, but could provide a better understanding of the pathologies that afflict segments of the human population (Newman & Symmes, 1982; Snowdon, 1978a; 1982).

The application of terminology usually reserved for descriptions of human speech to the vocal behavior of other species and the attribution of similar underlying cognitive and motivational states to both human and nonhuman animals has been criticized as being anthropomorphic. Anthropomorphism is probably encouraged by similarities in structure and behavior between humans and other primates arising from a common phylogeny (Asquith, 1984). These similarities are especially evident with regard to the common possession of neural laterality, vocal learning, phonetic syntax, lexical syntax, and semanticity (Asquist, 1981; Cleveland & Snowdon, 1982; Green, 1975; Marler, 1985).

Morton (1975) has discussed the role of the emotional substrate in influencing the structure of vocal signals in several groups of animals, while Waser and Brown (1986) have discussed the role of the physical habitat in influencing the structure of primate vocal signals. The insights into vocal morphology provided by these researchers suggest that contemporary human vocal behavior is an adaptation to the ecological conditions within which early hominids lived (Lieberman, 1977).

Although nonhuman primates lack the anatomical apparatus to produce the range of sounds required for the production of speech, many nonhuman primates can produce complex vocalizations. Human beings exhibit an elaboration of the supra-laryngeal musculature which facilitates the post-lingual modification of vocalizations. The degree of neuromotor control over the supra-laryngeal musculature and attendant vocal abilities of some nonhuman primates and those of neonatal humans are roughly equivalent, implying that these animals might serve as models for the development of speech in humans.

Most primates, including humans, employ the lips, teeth, tongue, and pharynx to modify the output of the larynx. These structures are employed to alter the areal function of the supra-laryngeal vocal tract, changing minima and maxima along its length, emphasizing and attenuating specific frequencies to create formant frequencies (Lieberman, 1977).

Compared to adult humans, nonhuman primates usually possess thin tongues, poorly developed esophageal musculature, a larynx positioned relatively high in the throat, an incipient pharynx incapable of extensive frequency modulation, and only modest neuromotor control over these elements of their vocal tracts. Nonetheless, nonhuman primates are capable of producing a wide range of morphemes and phonemes. This ability is not observed in avian subjects, which are featured in much of the research on the vocal behavior of nonhuman animals. Consequently, in order to establish a common psychological framework from which to investigate the origins and pathologies of human speech, the vocal behavior of primates should be increasingly emphasized.

Nonhuman primates possess specific loci in the central nervous system for the control of vocal behavior (Ploog, 1981), exhibit a trend toward neural lateralization of speech production centers (Green, 1975), and show categorical perception of communicatively significant sounds (Snowdon, 1978), all of which are characteristic of vocal communication in humans.

The size and complexity of the vocal repertoires of nonhuman primates appear to be larger than early research suggested and continues to expand as the equipment used to analyze them improves (Byrne, 1982). The vocal repertoires of animals possessing complex social systems have been determined to be especially complex.

The finding that the vocal repertoires of nonhuman primates are more complex than previously supposed could be an artifact of the misconceptions of early researchers, who operated under the assumption that vocal signaling was exclusively under the influence of the emotional substrate of the vocalizing animal--that is, entirely affective in nature. Contemporary research suggests that there is also a cognitive component to vocal signaling in many primates. This contention is supported by the observation that there is symbolic signaling in at least a few species of primates, e.g., vervet monkeys an assumption based on an apparent deemphasis in the iconicity and increased arbitrariness of some of its signals (Marler, 1985).

Recently, the structure and function of primate vocalizations have been extensively studied and reviewed (Morton, 1975; 1977; Snowdon, 1986; Waser & Brown, 1986; Wiley & Richards, 1978). In an attempt to consider all elements contributing to the structure and function of vocal signals, researchers have proposed schemes to guide the study of vocal communication. Contemporary scientists consider an act of vocal communication to consist of at least four elements: the physical structure of the signal, the motivational state of the signaler, the meaning of the signal, and the function or reason for producing the signal. Throughout this discussion, the term signal refers to the physical form of a communicative act, e.g., sound in the form of vocalizations (Sebeok, 1977).

The motivational state of an organism refers to underlying emotional conditions that predispose animals to emit particular vocalizations. Though emotional states are difficult to quantify, changes in physiological parameters can be correlated with specific classes of vocalizations. The meaning of signals can be inferred from the context within which they are employed and by changes in the behavior of recipient animals. The function of signals refers to the adaptive or evolutionary advantage conferred on organisms emitting or receiving them (Altmann, 1967).

Early studies, constrained by primitive equipment, probably underestimated the number of distinct call variants and categories in the vocal repertoires of nonhuman primates. The improved resolution of modern equipment has resulted in an apparent increase in the size and complexity of these repertoires. For example, Green (1975) found that the "coo call" of Japanese macaques, which was traditionally treated as a unitary, invariant vocalization, actually encompassed seven functionally distinct variants, each correlating with a specific social context. The detection of subcategorical variation in responsiveness to apparently unitary calls has also been detected in the response of pygmy marmosets to variants of conspecific trill calls (Snowdon & Pola, 1978), in the response of cotton-top tamarins to variants of conspecific chirps and long calls (Cleveland & Snowdon, 1982), and in the response of vervet monkeys to the grunts of conspecifics (Cheney & Seyfarth, 1982).

This improved perspective on the acoustic structure of calls has inspired research into the constraints imposed by natural acoustic habitats on call morphology (Waser & Brown, 1986; Wiley & Richards, 1978). Finally, the improved ability to quantify call morphologies precisely could enable taxonomists to employ vocal structure as an additional aid in the resolution of unclear taxonomic relationships (Hodun, 1981; Snowdon, Hodun, Rosenberger, & Coimbra-Filho, 1986). The increased amount of research into the vocal behavior of primates has expanded the understanding of the content of vocal messages.

One primary component of vocal communication is affective, reflecting the internal state of an organism, primarily its emotional disposition (Zahavi, 1982). Another component of vocal messages involves external referents (Seyfarth & Cheney, 1980; Smith, 1981). Vocal messages can contain information about the signaler, including its age, sex, emotional state, reproductive condition, species, deme, troop, and its individual identity.

The actual size of vocal repertoires is a subject of continual discussion. The resolution of vocal taxonomies is subject to interpretation and is influenced by the tendencies of individual researchers to lump or split vocal elements, greatly influencing the size of particular vocal repertoires (Altmann, 1967). Species exhibiting signal structures characterized by categorical, discrete, nonoverlapping acoustic units possess larger repertoires than those featuring more graded vocal signals (Marler, 1985). Complicating the understanding of vocal communication is the difficulty of distinguishing between the production of categorical signals and their perception. Whether or not a species possesses a categorical repertoire, it might exhibit categorical perception of acoustic signals.

The elucidation of vocal repertoires in nonhuman primates typically involves introducing a signal to an animal and recording its response, at which time an hypothesized function is assigned to the signal (Altmann, 1967). Often, the natural categorical responses of subjects do not coincide with those imposed on the behavior by researchers (Seyfarth & Cheney, 1980). Natural categories can be more precisely identified by manipulating individual call parameters to determine their relative importance in categorical perception. These procedures sometimes involve the application of artificially manipulated call elements to particular subjects.

For example, when pygmy marmosets are presented with artificially manipulated and naturally derived versions of "open mouth trills" and "close mouth trills," they are able to distinguish between artificially manipulated and naturally derived vocalizations. The trills are emitted in very different situations, the "closed mouth trill" during affiliative interactions and the "open mouth trill" during agonistic encounters. The primary distinguishing characteristic between the calls is their total duration, with the "closed mouth trill" having a mean duration of 176 milliseconds (ms) and the "open mouth trill" having a mean duration of 334 ms. Analysis of a distribution of the lengths of both call types reveals that all "closed mouth trills" are shorter than 250 ms and that all "open mouth trills" are longer than 250 ms. When the duration of trills is artificially manipulated, there is a well delineated categorical boundary--as determined by the response of the marmosets--to calls with durations between 247 ms and 257 ms, implying that this range encompassed the perceptual boundary between call types (Snowdon & Pola, 1978).

Goeldi's monkeys demonstrates similar perceptual abilities, though in this instance the critical parameter is the frequency range of the call. Goeldi's monkeys typically emit at least two types of alarm vocalizations, differentiated by frequency range, each of which can be synthesized and presented to subjects. Animals presented with alarm calls featuring a frequency range of 1.4 kHz to 2.4 kHz typically respond by emitting warning calls. When they are presented with nearly equivalent calls featuring a slightly higher frequency range of 2.6 kHz to 5.6 kHz they usually respond by freezing. The critical range of frequencies implicated in changing the perceptual category for these calls occurs between 2.4 kHz and 2.6 kHz. Systematic variation of other call parameters does not result in significant changes in the responses of Goeldi's monkeys (Masataka, 1983a).

Cotton-top tamarins appear to be able to distinguish between at least two variants of their "chirp" calls and respond differently to calls featuring slightly different durations. One relatively long variant functions as an intergroup spacing call, while a slightly shorter variant functions as an intratroop contact call (Snowdon, 1986).

Japanese macaques appear to possess a categorical repertoire and perceive the vocalizations of conspecifics categorically. These monkeys produce calls showing structural variability reliably corresponding to specific social situations and which elicit predictable responses from recipients (Green, 1975).

Signal Structure and Function

Morton (1977) suggests that avian and mammalian vocal morphologies are regulated by a specific set of motivational and structural rules. Broadly, low frequency vocalizations or those that are descending in pitch are highly correlated with aggression and agonistic behaviors. Lower pitched sounds suggest a larger body size and a more confident disposition. High frequency vocalizations or those rising in frequency are correlated with submission or affiliative behaviors. These sounds suggest small body size, immaturity, and tension resulting from uncertainty. Broad-band sounds, which are subjectively harsh sounding, are highly correlated with agonism and aggression, while pure tones are highly correlated with appeasement and affiliation.

Increasing frequency is highly correlated with decreasing hostility or with an increasing tendency to become submissive, while decreasing frequency is correlated with increasing hostility. The presence of components from both general classes of signal suggests conflicting motivational states. When there is motivational ambivalence, for example in mobbing situations, a particular type of call is emitted. These calls probably arose through the modification of long calls or territorial calls.

Vocalizations associated with agonism and aggression often possess a rhythmic structure and are almost perfectly graded (Rowell & Hinde, 1962). They are also the least species-specific of all classes of calls. As the level of arousal increases, the period of the rhythmic component decreases while the high frequency component is accentuated. The fundamental frequency of the vocalization also rises with the intensity of the encounter, often terminating in shrill screams. Changes in temporal parameters correlate with physiological responses to the situation, e.g., increasing in frequency as the respiratory rate accelerates (Rowell & Hinde, 1962). Higher pitched calls might arise ontogenetically from infantile "frustration" vocalizations and persist into adulthood to indicate the same emotion (Morton, 1977).

In addition to reflecting the internal motivational state of an organism, there are external referents associated with acts of communication. For example, communication can inform recipient animals about the who, what, and where of the signaler (Smith, 1981). External referents can take the form of other animals, including conspecifics and predators.

The morphology of vocalizations can be varied to convey information about these referents. Some species emit specific alarm calls to indicate the detection of certain classes of predators. For example, vervet monkeys appear to produce three alarm call variants in order to indicate terrestrial, arboreal, or aerial predators (Cheney & Seyfarth, 1985).

Variation in the morphology of particular classes of calls can be employed in the recognition of individuals by other members of its group. Squirrel monkeys emit affiliative "chuck calls" that are responded to differently by closely related animals and non-related group members. Variation in call parameters, including start and peak frequencies, provides a unique vocal signature for each individual (Smith and Newman, 1982). Similar group specific vocal characteristics enable mustache tamarins to differentiate between "long calls" of troop members from those of nontroop members, even when not in visual contact (Snowdon & Hodun, 1985). The sophistication of communication systems is often correlated with the complexity of social systems. One adaptive function of complicated vocal repertoires is to facilitate information exchange between potentially aggressive animals without requiring their close proximity.

In instances where large dominant species compete with smaller species, vocal behavior can be used to reduce aggressive physical interactions. Primates species which are typically more aggressive than other sympatric species often possess contact calls characterized by broad-band energy distributions, imparting subjectively harsh qualities to them. Highly social species, which often form large troops, possess contact calls with restricted energy distributions, imparting subjectively tonal qualities to them. It is conceivable that the large number of primates existing in South and Central America functionally partition niches on the basis of variation in vocal morphology more than by differences in physical attributes (Morton, 1977).

Primates living in forest habitats possess more discrete categorical vocal repertoires than those inhabiting open woodland or savanna habitats (Marler, 1977; 1985). Graded vocal repertoires facilitate signal flexibility at the expense of the precision possible with highly stereotyped repertoires.

Virtually any parameter, including fundamental frequency, harmonic structure, number and duration of discrete syllables, frequency modulation of elements, interelement intervals, and amplitude can be varied to alter the structure or function of vocal signals. Each parameter can vary continuously, making classification unwieldy, if not impossible. Classification based on behavior is problematic; animals do not necessarily recognize the categorical distinctions imposed on their vocal repertoires by researchers, especially where intercategorical distinctions are concerned (Marler, 1982). Presumably, nonhuman animals are more sensitive to between-category variation than within-category variation. As research continues, repertoires expand, with their sizes often dependent on the resolution of analytical apparatus and proclivities of individual researchers as much as on the responses of subjects.

Some researchers (Moynihan, 1970) insist that primates typically possess fewer than 20 distinct vocalizations, while others (Snowdon, 1982) have proposed repertoires featuring as many as 38 distinct vocalizations.

Species with graded repertoires show fewer distinct vocalizations than those featuring discrete repertoires. Those vocalizations associated with temporal emergencies possess the least amount of variation across taxa, e.g., alarm and mobbing calls, suggesting a high degree of convergence. These calls are structured to permit rapid diffusion throughout the environment while providing few acoustic cues to the location of the source. The greatest degree of divergence is found in calls requiring more species-specificity, especially those associated with reproduction and social affiliation. Territorial calls, while similar among closely related taxa, exhibit greater divergence when related taxa are distributed sympatrically. High degrees of convergence probably arise from common autonomic influences on vocal behavior within similar taxa (Morton, 1977) and from constraints imposed on vocal morphology by similar acoustic habitats (Waser & Brown, 1986; Wiley & Richards, 1978). Similarities notwithstanding, there is no common taxonomy describing vocal behavior within the primate order, despite attempts to construct widely applicable schemes.

Although there has been research into the influence that natural habitats exert over the adaptive morphology of primate vocalizations (Waser & Brown, 1984; 1986; Wiley & Richards, 1978), the influence that captive environments exert on the morphology and expression of vocalizations in nonhuman primates has been less intensively studied.

For comparative purposes, research on primate vocal behavior should include subjects living in natural habitats and in captivity. Research based exclusively on free living primates could result in a sampling bias against softer, affiliative calls, and toward louder, territorial calls, which are more easily recorded in the field (Snowdon, 1986). Conversely, research conducted exclusively on captive primates might be confounded by basing assumptions on incompletely developed vocal repertoires associated with primates reared in inadequate physical or social environments (Altmann, 1967).

The influence of the historical physical habitat, the contemporary physical habitat, the immediate emotional context, and adaptive function all combine to influence the structures of vocalizations. Based on these assumptions, the structure and function of primate vocalizations should be viewed as products of natural selection, i.e., adaptive responses of organisms to their respective habitats and niches (Klump & Shalter, 1984).

Habitat Acoustics

To the extent that communication is defined as an association between the behavior of a signaler and recipient featuring the transmission of specifically patterned energy, any degradation in the signal or change in its precise patterning represents a reduction in its information content. To varying degrees, there is always more information in a signal at a transmitter than at a receiver, primarily due to the degradation of the signal in the form of noise. Noise is any error in the association of the variation in a broadcast signal arriving at a recipient organism not originating at a transmitting organism. This type of degradation reduces the signal to noise ratio and diminishes the ability of recipients to obtain information from signals. Not all signal deterioration arises from deviations from its original state during transmission; many errors can be a function of some quality of the receiver, and can result in poor detection or inaccurate discrimination.

An extremely low signal to noise ratio reduces the ability of a recipient organism to discriminate between information encoded in acoustic signals and other sources of noise in its habitat. The physical degradation of acoustic signals imposes limitations on vocal communication in certain types of environments (Waser & Brown, 1986; Wiley & Richards, 1978).

The power density of a wave diminishes as a function of the inverse of the square of the distance from the source to the destination. This phenomenon is termed spherical spreading and results in a 6.0 dB reduction in sound pressure with each doubling of the distance between the point of origin and destination of an acoustic signal, limiting its effective range. Typically, animals do not produce acoustic signals which diverge in a purely spherical pattern, primarily due to the presence of heterogeneities in their surroundings.

Sound energy is dissipated during its transmission through a medium of propagation by viscous losses, e.g., heat conduction and friction. This type of loss is temperature dependent; at 20°C, a signal of 8.0 kHz will be attenuated by 0.02 dB per meter. Signal attenuation also increases with increasing humidity. Acoustic signals are further degraded through atmospheric absorption of high frequencies, absorption of acoustic energy at the ground interface, scattering by micrometeorological and physical heterogeneities in the environment, and the deflection of acoustic energy within a stratified propagation medium.

Acoustic energy is lost at the boundaries between media with differing densities through diffraction, refraction, and reflection. These phenomena are a direct result of the different particle densities of various substances and the different velocities of sound as it is conducted within each propagation medium. Reflection involves the return of a wave to the source medium as it impinges on the boundary of a second medium. Diffraction involves the deflection of a wave as it impinges on the boundary of a second medium, often resulting in complex interference patterns arising from the scattering of the wave. Scattering can exert a frequency dependent attenuation on some portions of the acoustic spectrum, especially that above 3.0 kHz. Further, diffraction can increase the spreading of the wavefront, reducing the power density of the wave and diminishing the sound pressure level of the signal. Signal degradation is reduced when objects in the propagation path of the wave are smaller than one wavelength in diameter with the result that high frequency signals are subjected to more reflection than signals with lower frequencies (Morton, 1975; Wiley & Richards, 1978). Physical features in the habitat, e.g., leaves and branches, can degrade acoustic signals by behaving as force oscillators with resonant frequencies of from 200 Hz to

2.0 kHz. Objects in the environment with diameters of less than 10 cm attenuate signals with frequencies above 3.0 kHz. One consequence of this type of signal degradation is that signals with frequencies above 1.0 kHz are more attenuated in forest habitats than in open habitats. Atmospheric turbulence can produce nonstationary heterogeneities that result in frequency dependent attenuation of acoustic signals. Nonstationary heterogeneities can cause fluctuations in the amplitude of acoustic signals by augmenting them through reverberation. Reverberation is more prevalent in densely forested habitats than in open habitats.

As a wave propagates through a medium, multipath transmission can produce both destructive and constructive interference, influencing the amplitude of a signal at various points along the path of propagation. Amplitude modulated signals, especially those at frequencies below 1.0 kHz, are severely degraded by the influence of reverberation and the formation of standing waves.

The combination of these factors comprise the phenomenon of environmental attenuation, which degrades acoustic signals as they propagate from points of origin to recipients (Wiley & Richards, 1978).

In densely forested habitats, environmental attenuation appears to decline at frequencies between 1.5 kHz and 2.5 kHz, especially at heights below 15 feet (Waser & Brown, 1984). The fundamental frequencies of the vocalizations of most callitrichids fall between these frequencies. Species distributed in the lower layers of the forest canopy possess vocalizations with average fundamental frequencies of 1.48 kHz (sd=1.39), while those distributed in higher layers of the canopy exhibit primary vocalizations with average fundamental frequencies of 2.71 kHz (sd=5.519; Waser & Brown, 1986; Wiley & Richards, 1978).

In open habitats, extremely low frequency signals are employed in long distance signaling. Signals with mean fundamental frequencies of 200 Hz are not uncommon and appear to propagate most effectively in open habitats, especially at elevations between 2 and 3 m above the ground (Waser & Brown, 1986).

Signal propagation efficiency is strongly influenced by the levels of ambient noise typical for various types of habitats, which determines the modal sound pressure levels, influencing the effectiveness of acoustic signals. Noise is present in discrete bands of energy and temporally patterned within each habitat type. Ambient noise levels are highest in riverine habitats and lowest in savannah habitats.

In riverine habitats, at 06:00 hours, the sound pressure level averages 27 dB. At 07:00 hours, as the ambient temperature rises, the sound pressure level reaches 32 dB, occasionally exceeding 37 dB. The increase in ambient noise between 2.0 kHz and 4.0 kHz arises largely from bird and insect noise, while that near 1.0 kHz results from the rustling of leaves. Insect stridulation produces a wide band of noise ranging from 4.0 kHz to 8.0 kHz (Waser & Brown, 1986).

In the savannah, at 06:00 hours, the ambient noise level averages 20 dB, rising to between 30 dB and 36 dB during the middle of the day. Virtually all of this increase is a result of wind noise. In the rain forest, the ambient noise level at 06:00 hours averages 27 dB, rising to between 33 dB and 40 dB at 15:00 hours. Although some biotic noise contributes to this increase, most of it arises from wind and the rustling of leaves (Waser & Brown, 1986). In rain forests, scattering accounts for most of the environmental attenuation, while in savannahs, absorption accounts for most attenuation (Waser & Brown, 1986; Wiley & Richards, 1978).

The physical nature of habitats imposes constraints on the structure of vocalizations by differentially degrading signals of different frequencies (Waser & Brown, 1986; Wiley & Richards, 1978). Vocal signals fall into two broad categories: those that feature the frequency modulation of a few narrow bands of frequencies, and those that feature the amplitude modulation of a relatively broad band of frequencies. Repertoires emphasizing amplitude modulation are relatively restricted and susceptible to degradation through reverberation and reflection. Vocal repertoires that emphasize frequency modulation are usually larger than their amplitude modulated counterparts and are able to convey more information through the selective modulation of specific bands of energy, either simultaneously or sequentially (Marler, 1977). Graded vocal repertoires, featuring relatively low frequency, amplitude modulated signals, are usually found in open habitats, while more categorical repertoires, featuring high frequency, frequency-modulated signals, are found in forested habitats. All Callitrichids inhabit relatively complex forested environments. Their vocal repertoires are comprised of high frequency, frequency modulated elements. This is especially true with those elements of their vocal repertoires important in long range communication. Signals featuring frequencies between 1.0 kHz and 4.0 kHz propagate most effectively through typical forest habitats with the least amount of degradation due to scattering and reverberation (Wiley & Richards, 1978). Generally, low frequency signals are optimal for long distance communication while higher frequency signals are optimal when source locatability is required. Low frequency vocalizations propagate for longer distances than high frequency vocalizations with equivalent amplitudes. Higher frequency signals are more rapidly degraded through interactions with heterogeneities present in certain types of habitats, especially those characterized by vegetative complexity (Wiley & Richards,1978). Nonetheless, many species employ high frequency vocalizations, especially when the locatability of the source confers an adaptive advantage on the signaler.

Despite their increased degradation in dense foliage, specific frequencies of sound are less degraded through attenuation than contemporary environmental acoustic models predict. In tropical forests, frequencies between 500 Hz and 2.5 kHz are attenuated less than frequencies above and below this range. This phenomenon, termed a "sound window," probably results from a large temperature gradient between the ground and upper canopy, which functions as an acoustic lens, focusing or reflecting acoustic energy downward, preventing its divergence into the atmosphere (Waser & Brown, 1984).

Within the Callitrichidae, only cotton-top tamarins and Geoffroy's tamarins possess long calls which conform to this prediction. The long calls of all other callitrichids feature slightly higher fundamental frequencies than those suggested as optimal by the "sound window" model (Cleveland & Snowdon, 1982; Moynihan, 1970; Waser & Brown, 1984).

The attenuation of calls important in long range signaling, especially territorial long calls, is further reduced if the calls are emitted in the morning, before the masking effects of environmental sounds become intrusive (Waser & Brown, 1986). The amount of noise originating from wind, insects, and vegetation rises as the ambient temperature increases. The masking influence of these sound sources is particularly severe at frequencies between 5.0 kHz and 8.0 kHz, reducing their effectiveness for use in long distance communication (Waser & Brown, 1984).

The assumed adaptive function of vocal signals, the motivational state of the signaler, and constraints on call morphology imposed by features of different acoustic habitats conspire to dictate the morphologies of vocal signals. Strong support for the contention that vocal morphologies are influenced by their adaptive functions and habitat constraints is provided by the highly convergent vocal morphologies of many forest dwelling birds and primates, especially Callitrichids (Vencl, 1977). Additional evidence for the influence of acoustic habitats on vocal morphology is provided by the finding that many primates emphasize pure tone vocalizations in habitats where scattering, insect stridulation, and leaf rustling are the predominant sources of environmental attenuation, while those dwelling in variable edge habitats, where these sources of attenuation are reduced, emphasize more frequency modulated vocalizations (Waser & Brown, 1984).

One primary effect of environmental attenuation is its influence on cues to the locatability of sound sources. The ability of an animal to locate a source of sound is determined by differences in the intensities and times of arrival of signals at each ear, a process enhanced by signals featuring high frequencies or transients. Scattering of high frequencies reduces the locatability of sound sources, while reverberation can obscure the transient elements of signals.

The structures of some signals important in social communication are strongly influenced by these considerations. Vocal signals employed in territorial displays are often structured to maximize transmissibility over long distances, while enabling recipients to localize their source. Calls specifically adapted for distance communication, intergroup spacing, and intratroop spatial regulation are generally termed "long calls," and have been described for every Callitrichid studied to date. For example, the cotton-top tamarin features two long call variants in its vocal repertoire, one important in intergroup territorial interactions and one important in intragroup cohesion (Cleveland & Snowdon, 1982). Calls important in group cohesion often possess structures which enhance the locatability of the source. For example, the pygmy marmoset employs three distinct types of trills, depending upon the distance between communicating animals, and varying in parameters which influence the locatability of the source (Snowdon & Hodun, 1981). Quiet trills, which feature minimal frequency modulation and time of onset cues, are emitted when animals are closest together, while "J" calls, featuring extensive frequency modulation and time of onset cues, are emitted when animals are farther apart. In the cotton-top tamarin, there are two variants of the single whistle and the multilevel whistle. The variants of each call emitted by animals in close proximity feature reduced frequency modulation compared to variants of the same calls emitted when animals are more distant from one another (Cleveland & Snowdon, 1982). Pygmy marmosets also emit calls important in intragroup spacing. The "closed mouth trill" is emitted antiphonally by foraging individuals, allowing them to assess the relative distances of other group members, preserving group cohesion without the need to maintain visual surveillance. Another trill variant, the open mouth trill, is emitted during agonistic encounters and results in aroused animals increasing their interindividual distances (Snowdon & Hodun, 1981). Calls employed in mobbing situations also feature cues that enhance their locatability. Mobbing calls are often sharp whistles or trills emitted to the perceived presence of predators. Callitrichid mobbing calls are characterized by short onset and offset times and considerable frequency modulation (Epple, 1968; Moynihan, 1970). The high degree of frequency modulation increases the locatability of the source, enabling conspecifics of the vocalizer to locate it and to participate in harassing the target animal.

Conversely, alarm calls tend to possess structures that minimize the locatability of the source, including relatively short durations, high frequencies and minimal frequency modulation. The absence of frequency modulation and the scattering of high frequencies by stationary heterogeneities diminishes the locatability of the vocalizer to potential predators.

Alarm calls and affiliative vocalizations used at extremely close range are often slightly graded, structured to minimize the locatability of the source, reducing the possibility of its detection by predators. Conversely, mobbing calls are structured to enhance the detectability of the signaler, enabling conspecifics to converge on its location to assist in harassing the predator. Occasionally, other predators are attracted to the call, foiling the attack (Klump and Shalter, 1984). Alarm calls possibly function to increase the inclusive fitness of individuals related to signalers through mutual alerting, reducing the probability of their succumbing to predation. Mutual alerting and predator deception have been observed across a wide range of social species, ranging from pygmy marmosets (Snowdon, 1978; Snowdon & Cleveland, 1984; Snowdon & Hodun, 1981) to ground squirrels (Dunford, 1977), involving similarly structured vocalizations, and probably representing a case of vocal convergence (Vencl, 1977).

Locatability, however, is not always adaptive. Unlike mobbing calls, which require detectability to provide information to conspecifics about the location of a potential predator, alarm calls should offer some degree of ventriloquy to minimize the possibility of detection of the signaler by potential predators. Consequently, alarm calls feature characteristics which tend to reduce cues to locatability by decreasing phase information, minimizing interaural intensity differences, and decreasing interaural time of arrival cues (Marler, 1977).

The location of a signaler can also be obscured if vocalizations are emitted at frequencies beyond the perceptual ranges of major predators. Pygmy marmosets emit variants of their trill calls, when animals are in close proximity, that feature a fundamental frequency well above the hearing range of major avian predators. These calls are also above the frequency range of typical ambient environmental noise, providing pygmy marmosets with an exclusive acoustic channel for close range communication (Snowdon & Hodun, 1981).

Recipient animals can often derive information about the distance of signalers through the amplitude, amount of reverberation, and high frequency attenuation of vocalizations. As the distance between a signaler and recipient increases, the ratio of direct to reflected sound decreases. There is an increase in the amount of reverberation, a decrease in the relative levels of higher frequencies, and a reduction in the amplitude of the signal (Wiley & Richards, 1978).

The influence of the environment on the structure of vocal signals is usually overlooked in research involving the presentation of acoustic variables to animals. Some acoustic influences arising from the habitat, including some forms of degradation, should be considered when playback variables are designed. Failure to consider environmental influences on signal morphology might result in the use of artificially simplified treatments with reduced environmental validity to the subjects, conceivably resulting in their failure to respond.

Meaning of Primate Vocal Signals

The meaning of a vocalization can be determined through playback experiments, the assumption being that the meaning of a vocalization can be inferred from the context within which it is used. The behavior of the communicating animals is observed before, during, and after the communicative act. The motivation of the signaler can be inferred from the assumed meaning of a signal, while the meaning of a signal can be inferred from the response of the recipients (Altmann, 1967). This experimental paradigm arises from the contemporary definition of communication, which suggests that it functions to allow organisms to modulate the behavior of others (Krebs and Davies, 1987).

This type of research has resulted in the finding that primate signals can convey information about warning, threat, identity, affiliation, emotional state, social context, and external referents. In some instances, a single vocal signal is associated with several perceptual categories, while in others a single signal can convey a range of messages within a single category.

The motivational state of an animal can influence the morphology of its vocalizations. Emotional state is often correlated with the tonicity of the pharyngeal-laryngeal musculature, influencing the frequency and inflection of vocalizations (Altmann, 1967). Changes in inflection can allow group members to assess the emotional state of signalers. The intensity of messages can be augmented by accompanying locomotor activities, e.g., head shaking (Zahavi, 1982).

These trends in the expression of intensity agree with the predictions of Morton (1977) that harsh sounding low frequency vocalizations, descending in frequency, are correlated with increasing threat or agonism, while high frequency vocalizations, increasing in frequency, are correlated with appeasement, affiliation, or decreasing threat.

In addition to reflecting the internal emotional state of animals, vocalizations can possess symbolic or semantic qualities associated with environmental phenomena, termed external referents. External referentiality and semanticity are suggested by the correlation of specific vocal signals with predictable features of the environment (Marler, 1985; Smith, 1981). These phenomena have been extensively studied through playback experiments with vervet monkeys, which emit one of three distinct alarm calls, depending on the type of predator detected: snakes, eagles, or leopards (Seyfarth et al., 1980; Struhsaker, 1967). Alarm calls associated with each class of predator were played to free-ranging animals, which responded distinctly differently to each type of alarm. In response to eagle alarms, animals vacated arboreal perches and sought ground cover; in response to snake alarms, animals engaged in increased terrestrial surveillance; and in response to leopard alarms, the animals migrated from the ground into arboreal refuges. Similar findings have been obtained with Goeldi's monkeys, which emit two alarm call variants, one eliciting mobbing behavior and the other eliciting freezing (Masataka, 1982). Cotton-top tamarins also emit variants of structurally similar chirps to various classes of threatening phenomena, differentially eliciting mobbing or alarm behavior (Cleveland & Snowdon, 1982).

The degree of convergence between the alarm and mobbing vocalizations of sympatric species is relatively high, while those associated with social cohesion are more species specific, often even varying at the subspecific level (Masataka, 1983b). The similarities of some classes of vocalizations between sympatric species facilitates interspecific communication. For example, antipredator calls of Goeldi's monkeys are structurally similar to those of the sympatric saddleback tamarin and red-bellied tamarin and elicit similar antipredator responses from both species (Masataka, 1983b). Similar interspecific responsiveness to the vocalizations of sympatric species has been observed between the mustache tamarin and the emperor tamarin of western Amazonia (Terborgh, 1983).

If convergent vocalizations are the rule for signals associated with temporal emergencies, then variation is the rule for those associated with reproduction and social cohesion. In a study of four sympatric subspecies of saddleback tamarin Hodun et al., (1981) observed that each exhibited structural differences in several syllables of their long calls. The four subspecies, *Saguinus fuscicolis fuscicolis*, *S. f. iwagery, S. f. lagrinotus*, and *S. f. negriphones*, exhibited significant differences in the initial and terminal frequencies of their long calls, with those of *S. f. iwagery* and *S. f. negriphones* representing the extremes. Despite the differences in long call structure, individuals from each subspecies responded to the long calls from individuals of other subspecies. Since these tamarins do not regularly interbreed in the wild, the probability that these dialects function as reproductive isolating mechanisms is minimal; it is more probable that they represent epiphenomena that function to identify troop members.

Cotton-top tamarins also demonstrate the ability to distinguish the calls of troop members from those of unfamiliar animals. When cotton-top tamarins hear the long calls of strange animals, they respond with behaviors indicative of elevated levels of arousal (Snowdon & Hodun, 1985).

The degree to which variation in vocal morphology is genetic or learned is not clear, and appears to be dependent on both the species in question and the particular class of vocalization under study. While the variation observed in the long calls of sympatric saddleback tamarins suggests vocal learning (Snowdon & Hodun, 1985), other research suggests that some vocal behavior is strongly genetically mediated, though the degree of genetic versus ontogenetic contributions remains unclear. The genetic control of vocal behavior has been investigated in infant squirrel monkeys. Newborn Roman arched and gothic arched squirrel monkeys, two distinct subspecies, emit correctly formed "isolation peeps," distinctive for their respective subspecies, even if deafened prior to hearing vocalizations from other animals. Hybrids of the subspecies emitted isolation peeps which were structurally intermediate between the forms produced by parents of different subspecies (Newman and Symmes, 1982).

The ability of isolate-reared infants to respond correctly to the alarm calls of adult females upon hearing them for the first time strongly suggests that there is a genetic component to their acquisition of vocal behavior. Their responsiveness to "alarm peeps" is enhanced if they are simultaneously presented with the image of a terrestrial predator, suggesting that there is some visual facilitation in the acquisition of extremely critical vocal behavior (Herzog & Hopf, 1984).

Considerable research has focused on the ontogeny of vocal behavior. There are several examples of juvenile vocalizations emitted exclusively by infants and immature animals which will develop into adult forms only gradually. For example, infant Japanese macaques emit distinctly juvenile variants of the "coo call" to solicit contact or nursing from their mothers (Green, 1975). In infant tamarins and marmosets, a modified adult long call functions as a general alarm call (Snowdon, 1986).

Many young primates, including Callitrichids, exhibit a type of vocal practicing which resembles babbling, characterized by the novel juxtaposition of adult forms of vocal elements (Snowdon, 1986). Young vervet monkeys often emit alarm vocalizations to non-threatening objects or to incorrect classes of predators. As young animals mature, alarm calls are emitted with increasing precision, probably through practice and the nonreinforcement of inappropriate vocal behavior (Seyfarth et al., 1980).

Research into the reinforcement of vocal behavior in agile gibbons suggests that the presentation of conspecific vocalizations to these animals increases their rate of vocal activity through classical conditioning (Maples & Haraway, 1982).

Vocal development through social learning has been observed in Japanese macaques in the cultural transmission of troop-specific feeding calls (Green, 1975). Hodun (1981) reported that saddleback tamarins demonstrate a degree of vocal learning. In an area where the territories of four sympatric subspecies, *S. f. fuscicolis, S. f. iwagery, S. f. lagrinotus,* and *S. f. negriphones* adjoin, individuals often possessed vocal repertoires featuring mosaics formed from elements derived from the repertoires of the other subspecies. Since these animals do not typically interbreed, there appears to be no genetic contribution to the formation of these novel repertoires, suggesting that they are learned.

The importance of the social environment in the development of a normal adult vocal repertoire has been investigated in several species, though the findings might not apply to all primates. Generally, animals reared in social isolation demonstrate profound deficits in vocal competency. For example, isolation-reared rhesus macaques emit normally affiliative "coo" vocalizations with abnormal amplitudes, inflections, harmonic structures, and temporal parameters, often within inappropriate social contexts (Newman & Symmes, 1982).

Deficits in the morphology of vocalizations have important implications for nonhuman primates. Vocalizations are apparently critical in the identification of infants by mothers and in the establishment of a troop identity. The ability to establish the identity of others exclusively through acoustic channels is important in the dense foliage of temperate and tropical forests, the habitats of most primates. The preferential identification of related animals probably facilitates kin selection, particularly important in the interactions between parents and their offspring. For example, adult female squirrel monkeys are able to discriminate the isolation peeps of their own infants from those of unrelated infants, even after a separation period of two weeks (Symmes & Biben, 1985). Female vervet monkeys will orient toward a speaker from which emanates the vocalizations of their own infant, while nearby adult females fail to do so (Seyfarth et al., 1980).

The ability of adult Callitrichids to identify individuals through their vocalizations has been observed in several species. Pygmy marmosets exhibit individual variability in the structure of several contact calls, including the "J" call and the "closed mouth trill," both of which are implicated in individual recognition and intratroop cohesion. Marmosets hearing these calls demonstrate recognition of the vocalizing animal by orienting toward and often approaching the source (Snowdon, 1986). Similar phenomena have been observed in the common marmoset where variability in one or more parameters of their contact calls, including duration and initial to terminal frequency range appears to provide individuals with unique vocal signatures, enabling other marmosets to identify them reliably (Snowdon & Cleveland, 1980). Cotton-top tamarins also appear able to identify other individuals reliably, based on the uniqueness of their territorial long calls (Snowdon, 1983).

Distinctive vocal morphology can also function in the recognition of troop members. Mustache tamarins respond differently to the calls of troop members than to those of unfamiliar animals (Snowdon & Hodun, 1985).

The complexity of primate vocal repertoires suggests that there must be grammatical rules for assembling the large number of elements comprising their vocal repertoires into discrete signals. Recent research on the vocal behavior of nonhuman primates suggests that some species regularly recombine vocal elements in predictable ways to form different messages, implying the existence of grammatical rules for their recombination (Cleveland & Snowdon, 1982). Syntactical rules are suggested by the apparent importance of the order of vocal elements in a sequence. Two types of syntax, phonetic and lexical, have been discussed by Marler (1982).

Phonetic syntax involves the formation of phonetic elements, termed morphemes, from sounds that possess no intrinsic meaning. Morphemes are then combined to form unique vocal messages, e.g., words, through the recombination of phonetic elements. The usurpation of initially meaningless sounds for the transmission of information represents a type of elemental openness. The proper sequencing of these signals into meaningful sequences, e.g., words into sentences, represents lexical syntax. The recombination of higher order elements into complex messages represents secondary openness. In considering phonetic syntax, the meaning of each phonetic element is not altered by its position in a novel sequence. However, with lexical syntax, the meaning of the sequence of lexical elements is influenced by their order.

While examples of phonetic syntax exist in the primate literature, clear examples of lexical syntax exist only in human speech (Marler, 1982). Altmann (1967) has stated that this duality of patterning is extensive in, and a unique characteristic of, human speech. Examples of apparent phonetic syntax have been reported in the long calls of saddleback tamarins (Hodun, Snowdon, & Soini, 1981), Geoffroy's tamarins (Moynihan, 1970), and cotton-top tamarins (Cleveland & Snowdon, 1982).

The vocal behavior of the cotton-top tamarin suggests the presence of phonetic syntax and other complex structural rules, including: an allowance for the ad libitum repetition of all call elements; the requirement that all short, frequency modulated elements precede longer, less modulated elements; and the requirement that the fundamental frequency of structural elements decreases throughout the duration of a call (Cleveland & Snowdon, 1982). The meaning of vocal signals formed from the combination of other, situationally distinct calls appears to be intermediate between the meanings of the source vocalizations. A similar phenomenon has been observed in capuchin monkeys. These animals often emit a derived vocalization consisting of three situationally distinct call elements to form a vocalization with a meaning intermediate between those of its constituent parts (Robinson, 1979).

The ordering of vocalizations has been observed in several species, especially those exhibiting dueting, e.g., siamangs and agile gibbons (Haimoff, 1984), common marmosets (Snowdon & Cleveland, 1984), and tamarins; Cleveland & Snowdon, 1982).

The dueting of agile gibbons is strictly ordered and appears to be important in territorial defense and in pair bond maintenance. The female often initiates calling with relatively simple call elements. When the male responds, she introduces increasingly complex call elements. The animals then alternate their vocal activity until the male responds with his most elaborate loud call (Raemaekers & Raemaekers, 1985). Similar dueting behavior has also been reported for the titi monkey (Robinson, 1979).

Common marmosets exhibit a precise ordering to the emission of some classes of vocalization. If one animal emits a "closed mouth trill," it will not emit another until all of the others in its troop have vocalized in response. This sequential dependency might facilitate group cohesion and integrity by allowing group members to provide locational information each time there is a bout of intratroop cohesion calling (Snowdon & Cleveland, 1984).

Free living pygmy marmosets exhibit similar behavior in the emission of contact calls while foraging. These animals appear to respond to one another with an ordered call sequence. Analysis of calling sequences in captive pygmy marmosets suggests that they also respond with a predictable sequence more often than would be expected by chance. The animals appear to follow the simple rule that each animal vocalizes once during a bout, with no individual repeating a call until all have participated. Once established, the call sequence is maintained throughout the bout (Snowdon & Hodun, 1981). These and other studies suggest that primate communication systems are more complex than early researchers proposed.

The nearly linguistic nature of the vocal behavior of many nonhuman primates becomes increasingly apparent as the knowledge of their communicative abilities grows. It becomes even more apparent when the vocal behavior of a single taxon, e.g., the Callitrichidae, is exhaustively investigated.

Vocal Communication in the Callitrichidae

The study of vocal behavior in Callitrichids began with the work of Epple (1968) on the common marmoset and several species of tamarin. Work on the communication systems within the taxon continued with that of Moynihan (1970) on Geoffroy's tamarins, Snowdon and Pola (1978) on pygmy marmosets, Moody and Menzel(1976) on saddleback tamarins, and Cleveland and Snowdon (1982) on cotton-top tamarins.

Although Moynihan (1969) claimed that there was a relatively low hypothetical limit to the size of the vocal repertoires of nonhuman animals, virtually all researchers working with Callitrichids reported repertoire sizes larger than Moynihan had suggested was possible. Conceivably, expanded vocal repertoires compensate for the reduced complexity of facial expressions observed in Callitrichids (Redican, 1975). The large repertoire size appears to result from the recombination of a few fundamental phonetic elements to form a considerable number of derived signals (Cleveland & Snowdon, 1982; Epple, 1968).

The morphology of Callitrichid vocalizations conforms to the structural rules proposed by Morton (1977), which suggest that some call parameters are influenced by the motivational state of organisms. Other features of call morphology are clearly adaptive responses to the physical habitats within which Callitrichids have evolved and function to facilitate transmissibility and to modify locatability (Waser & Brown, 1986).

Discrete signals can be grouped into two broad functional categories: predator alarm calls and group cohesion calls. Slight variations in signal parameters can alter the meaning of vocalizations to correspond with varying social contexts, a phenomenon also observed in other primates (Cleveland & Snowdon, 1982; Green, 1975; Masataka, 1983a).

The vocal repertoires of several Callitrichids feature examples of both phonetic syntax and grammatical rules reminiscent of lexical syntax (Cleveland & Snowdon, 1982).

Morphological variation in the vocalizations of Callitrichids is often manifested in the form of what appear to be local dialects which possibly function to reproductively isolate sympatric sub-species (Snowdon, 1985). Demographic variability in vocal morphology between allopatric populations of related species could also function in speciation, especially if genetically mediated vocal variability, reinforced by assortative mating and local variation in habitats, accelerates reproductive isolation and divergence (Waser, 1985).

Reliable vocal variation could serve taxonomists as additional characters in the resolution of the confused taxonomy of the Callitrichidae (Snowdon et al., 1986). This is especially true for those vocalizations that appear to be strongly genetically mediated, e.g., long calls. The application of variation in long call morphology to taxonomic questions has been attempted in golden lion tamarins (Snowdon et al., 1986), and saddleback tamarins (Snowdon & Hodun, 1981). The incorporation of vocal characters as taxonomic aids could resolve taxonomic uncertainties within the taxon, and could facilitate the maintenance of genetically pure populations of captive endangered primates.

Morphological parameters which vary across species and between call categories include number of syllables, syllable duration, initial and terminal frequencies, peak frequencies, frequency ranges, and the differences between peak, initial, and terminal frequencies. Any one or all of these parameters can be employed in the description and definition of vocal signals, which can then be assigned to the categories that constitute vocal repertoires.

A severe problem with comparing the work of researchers is their use of idiosyncratic vocal taxonomies. All of those who have worked on the vocal behavior of Callitrichids have employed slightly different vocal taxonomies. Occasionally, discrepancies can be resolved through an analysis of the social context within which a vocalization is recorded, or, in rare instances, spectrograms can be compared.

Unfortunately, researchers have often referred to different classes of calls with subjectively descriptive terms without providing accompanying quantitative data. Terms including peep, scream, screech, squeal, trill, twitter, and whistle, in addition to phrases including "canary like" and "flute like" have been applied to Callitrichid vocalizations (Cleveland & Snowdon, 1982; Epple, 1968; Hershkovitz, 1977; Moynihan, 1970). Vocalizations are occasionally described onomatopoeically, e.g., describing a contact call as a "tsee" call (Moynihan, 1970).

Fortunately, some elements of all of the proposed vocal repertoires are recognizably equivalent. Moynihan (1970) employs a vocal repertoire for Geoffroy's tamarins which feature functional categories similar to those proposed for cotton-top tamarins by Cleveland and Snowdon (1982).

When similar broad categories are discussed and accompanied by descriptions of the calls and their contexts, comparisons are possible. Even some findings from the early work of Epple (1968) are, with difficulty, comparable to later research, primarily because adequate descriptions are provided.

Moynihan (1970) criticized Epple's work for being inconsistent and lacking in quantitative information, rendering many of its findings difficult to corroborate with those from other research. Oddly, Moynihan (1970), some of whose work is also highly qualitative and incomplete, borrowed many of the functional categories for his vocal repertoires from Epple, rendering some of his findings equally problematic.

For example, tamarin alarm calls are referred to as "loud, long calls" by Moynihan (1970), "slicing chirps" by Epple (1968), and "A chirps" by Cleveland and Snowdon, (1982). Moynihan describes a "rasp" for Geoffroy's tamarins that is functionally equivalent to the "squawk" described by Cleveland and Snowdon for cotton-top tamarins and termed a "squeal" by Epple for both species. The "broken rasp" described by Moynihan for Geoffroy's tamarins is probably the "chevron chatter" described by Cleveland and Snowdon for cotton-top tamarins, and the "chatter" described by Epple for both species. Moody and Menzel (1976) describe the mobbing calls of saddleback tamarins as "squawks," yet they are the functional equivalents of the "A chirps" described for cotton-top tamarins by Cleveland and Snowdon.

Another major problem that inhibits comparisons of the work of Epple with that of later researchers is the use of an alternate taxonomy. Epple (1968) refers to her subjects as "*Odipomeyedus oedipus*" and "*Odipomyedus sphinxi*". Whether or not these are, respectively, the cotton-top tamarin and Geoffroy's tamarin is not clear.

Fortunately, some research utilizes behavioral and vocal repertoires with adequate descriptions of their operational definitions. In a comprehensive study of the red-bellied tamarin, Coates and Poole (1983) provide an extensive ethogram for their subjects which can be directly compared to other research. The research of Moody and Menzel (1976) on saddleback tamarins features a useful ethogram which overlaps that proposed by Cleveland and Snowdon (1982) for the cotton-top tamarin.

Irrespective of confusion about the taxonomies of their vocalizations, all of the research on the vocal behavior of Callitrichids suggests that there is a high degree of convergence in the structure and function of their calls. All Callitrichids emit chuck calls when foraging, trills when aroused, chatters during mobbing, atonal calls during submission, and low frequency calls when fearful. The degree of similarity between many Callitrichid vocalizations appears to increase when animals become aroused.

All Callitrichids seem to produce an alarm scream to the image of predators with durations ranging from 1.0 sec to 1.5 sec. All species emit a short, monosyllabic "isolation peep" when a cagemate is removed or when they are placed in isolation. These calls possess durations ranging from 0.48 sec to 1.1 sec and fundamental frequencies ranging from 1.25 kHz to 2.5 kHz. In cotton-top tamarins, as the level of agitation rises, these calls increase in duration and intensity, while decreasing in frequency. There is a concomitant increased emphasis on the third, fourth, and fifth harmonics, with considerable energy near 24.0 kHz (Epple, 1968). All species emit contact calls in response to disturbances, though cotton-top tamarins and Geoffroy's tamarins vocalize more variably and for longer durations than other Callitrichids. These calls range in duration from 0.057 sec to 0.24 sec.

When alarmed, most species emit multisyllabic contact calls, or trills, featuring rhythmic intensity fluctuations. The trills of cotton-top tamarins are the longest of any Callitrichid and consist of from two to 25 overlapping segments, each of which has an average duration ranging from 0.066 sec to 0.09 sec. The total call duration ranges from 0.19 sec to 0.85 sec, with an average frequency range of 2.0 kHz to 60 kHz. These calls, described by Epple (1968), are probably the "A trills" described by Cleveland and Snowdon (1982) which function as mobbing calls. When they are presented to other tamarins, they emit similar vocalizations (Epple, 1968).

Some of the trills of lion tamarins are functionally unique, often being emitted to elicit attention from cagemates or caretakers.

Submissive vocalizations, often termed "squeals," are emitted by individuals of all species when confronted by dominant animals. All species emit extremely short calls, often in association with feeding, ranging in duration from 0.019 sec to 0.026 sec (Epple, 1968), and termed "C chirps" in cotton-top tamarins (Cleveland & Snowdon, 1982).

Intergroup spacing calls are the most structurally conservative and least labile vocalizations within the Callitrichidae. Their individual uniqueness enables animals to identify other troop members accurately through their long calls. However, the long calls of Geoffroy's tamarins and cotton-top tamarins, which have been geographically separated from other tamarins for some time, are structurally distinctive (Snowdon & Hodun, 1985). The calls are whistles consisting of from 2 to 4 slightly frequency modulated syllables, ranging in duration from 600 to 800 ms with a lower frequency range of from 0.5 kHz to 1.0 kHz and a higher frequency range of from 2.5 kHz to 3.0 kHz, slightly lower than the contact calls of other tamarins. This variation might represent a special adaptation to a slightly less humid habitat, wherein lower frequencies are less attenuated than higher frequencies (Waser & Brown, 1984; 1986; Wiley & Richards, 1978).

Adult Callitrichids exhibit a relatively high degree of stereotypy in vocal behavior. This is not necessarily an artifact of genetic constraints on vocal behavior, but rather, a result of the possession of well developed categorical repertoires featuring discrete signals. Discrete signals are not necessarily indicative of primitive or simple communication systems, rather, the ritualization of signals represents an adaptation enhancing their predictability for communication in habitats where visual signals are often inhibited.

Vocal variability does exist within the taxon, especially in young animals (Epple, 1968). Some aspects of vocal behavior are subject to modification through learning. The acquisition of normal adult vocal behavior is critically dependent on adequate social experience. For example, immature Callitrichids often exhibit contextually inappropriate vocal behavior until they have acquired sufficient practice in vocalizing as they obtain increased social experience (Snowdon, 1986), a phenomenon also observed in immature vervet monkeys (Cheney & Seyfarth, 1985). Often, vocalizations must be emitted in the presence of relevant external referents, including conspecifics, before they are employed in appropriate social situations, a phenomenon also observed in infant squirrel monkeys (Herzog & Hopf, 1984).

The vocal repertoires of immature animals tend to be more graded and variable than those of adults, becoming more categorical as neural control over the musculature of the vocal tract develops. The modal frequencies of vocalizations tend to descend as young animals mature. As the amount of neural control over the subglottal musculature develops, the range of possible frequency modulation increases, resulting in the ability to produce higher frequency vocalizations than even those of infants (Ehret, 1980).

Within the Callitrichidae, the inexorable trend throughout ontogeny is toward a reduction in variability and toward greater precision through increased ritualization. This predictability in vocal behavior is sufficient to propose reliable repertoires for the vocalizations of all Callitrichids, including the cotton-top tamarin, which seems to exhibit greater variation in its vocal behavior than any other Callitrichid (Epple, 1968).

The Vocal Repertoire of the Cotton-Top Tamarin

Within the family Callitrichidae, two of the most well studied species are the cotton-top tamarin and Geoffroy's tamarin (Cleveland & Snowdon, 1982; Moynihan, 1970). These tamarins have demonstrated surprisingly complex vocal repertoires, larger than those envisioned by earlier researchers (Moynihan, 1970; 1976). The vocal repertoire of the cotton-top tamarin features a vocabulary composed of 38 distinct structural elements of two fundamental forms, chirps and whistles.

Chirps, described as short frequency modulated calls, are classified into eight distinct functional categories. Whistles, described as relatively long, constant frequency calls, are classified into five distinct functional categories. These discrete phonetic elements do not describe points on a motivational continuum; rather, each element functions in situationally distinct contexts. The combination and sequence of phonetic elements can be varied to increase the number of possible messages.

The recombination of phonetic elements to form novel signals appears to represent a form of phonetic syntax. Additionally, there are at least two examples of what is apparently lexical syntax, suggested by the formation of novel messages through the ordering of lexical elements (Cleveland, & Snowdon, 1982; Marler, 1977; Maurus, Pruscha, Wiesner, & Geissler, 1979).

Vocalizations recorded from a captive colony of cotton-top tamarins housed at The University of Wisconsin Regional Primate Center were translated into spectrograms. These were then analyzed to measure vocalization parameters, including initial, peak, and terminal frequencies, changes in initial, peak and terminal frequencies, presence or absence of stem upsweep, duration of individual call elements, total call duration, and mean intensity. The results were statistically analyzed to detect significant parametric differences between calls. Distinctly different calls were then assigned to hypothetical functional categories constructed on the basis of pilot playback studies. Hypothesized signal functions were confirmed or rejected based on the response of animals during a secondary sequence of playback experiments. In some instances, individual parameters were varied to observe their influence on the categorical perception of calls.

On the basis of this research, 38 distinct call elements, of two primary types, have been placed into six broad categories: single frequency modulated syllables, pulsed vocalizations, single whistles, multiwhistles, combination calls, and multiple calls.

Simple grammatical rules provide a mechanism for producing a relatively large number of discrete messages. For example, with messages featuring both chirps and whistles, chirps always precede whistles. The intensity of a message can be increased through the repetition of call elements. When repetition occurs, each succeeding segment features a slightly lower modal frequency than those preceding it.

The repertoire appears to feature examples of both phonetic and lexical syntax. Lexical syntax is exemplified in the structure of the "inverted U + whistle," composed of modified elements from an "E chirp," a general alarm vocalization often emitted in response to aversive stimuli, and modified elements from a "squeak," a low intensity vigilance call. The resulting "inverted U + whistle" is emitted during intermediate intensity vigilance behavior. Lexical syntax is also suggested in the structure of the "F chirp + whistle," formed from the combination of an "F chirp," an intertroop spacing call emitted in response to the presence of unfamiliar animals, with whistle elements from the "normal long call," which functions in intergroup spacing. The derived "F chirp + whistle" is apparently emitted by animals to apprise other troop members of the presence of unfamiliar tamarins, and to regulate the distance of the troop from the unfamiliar animals.

Tamarin vocalizations appear to conform to structural and motivational rules proposed by Morton (1977), which suggest that the morphology of vocalizations is modified by the emotional state of the vocalizer. For example, terminally modulated whistles and quiet long calls increase in median frequency throughout their respective durations, a characteristic typical of appeasement or affiliative vocalizations. Conversely, type "A chirp chatter," type "E chirp chatter," and "chevron chatter" calls all feature broad frequency bands, are subjectively harsh sounding, and are associated with arousal and irritability (Cleveland & Snowdon, 1982; Epple, 1968; Morton, 1977).

The morphology of calls is further dictated by the acoustic habitats within which they have evolved. Calls important in intertroop communication often feature high amplitudes and low modal frequencies, increasing their transmissibility. Calls important in close range intragroup cohesion often feature low amplitudes and minimal frequency modulation, decreasing their locatability. Those important in longer distance group cohesion often feature considerable frequency modulation to increase the locatability of the signaler (Waser & Brown, 1984; Wiley & Richards, 1978).

For example, "quiet long calls," important in close range intratroop cohesion, are characterized by low amplitudes, pure tonal qualities, minimal frequency modulation, and reduced transmissibility, while "normal long calls," important in longer distance group communication, are characterized by a greater amplitude and broader bands of frequencies.

The following classification scheme is derived from the work of Cleveland and Snowdon (1982) and is based on structural similarities, irrespective of functional considerations.

Class One Vocalizations: Single, Frequency Modulated Whistles

This class of vocalizations includes chirps, squeals, and slicing screams. These vocalizations consist of single syllable, chevron shaped frequency modulated units, comprising two broad call classes, short duration chirps and long duration slicing screams and squeals.

Eight distinct variants of chirp have been detected, "A," "B," "C," "D," "E," "F," "G," and "H," based on differences in their mean durations, fundamental frequencies, peak frequencies, peak to terminal frequency differences, presence or absence of stem upsweeps, and duration and frequency of downsweeps. Each distinct call is emitted within a clearly defined behavioral context.

A chirps: These calls consist of a single, frequency modulated syllable, 79.9 (± 29.7) milliseconds in duration which features a stem upsweep at 7.3 kHz, ascending to 8.7 kHz (±1.7kHz) and descending to 7.0 kHz. The terminal frequency is 2.7 kHz (±0.9 kHz) and the peak-to-end frequency difference is 5.9 kHz (±1.6 kHz). "A chirps" are emitted during mobbing situations. Tamarins emitting them exhibit piloerection of the head and tail, visual fixation on the target object, open mouth threats, and sporadic locomotor activity. Responding group members emit "A chirps" and "slicing screams" infectiously and behave similarly to the vocalizing animal. "A chirps" are emitted in response to sudden sounds or movements, though some groups emit them when presented with preferred items of food. They are rarely emitted in response to acoustic stimuli.

B chirps: These calls consist of a single syllable 100 ms (±25.9ms) in duration, including the stem upsweep. The initial frequency is 4.9 kHz (±0.9 kHz), the peak frequency is 6.0 kHz (±0.9 kHz), the terminal frequency is 4.0 kHz (±0.8 kHz), and the peak-to-terminal frequency difference is 2.0 kHz (±0.6 kHz). "B chirps" are emitted during directed environmental exploration. The vocalizer exhibits visual fixation toward the target object, often frowning. Other tamarins hearing this call seldom vocalize in response.

C chirps: These calls consist of a short ascending element, a longer descending element, and are 25.2 ms (±5.4 ms) in duration, including a stem upsweep. The initial frequency is 9.3 kHz (±1.2 kHz), the peak frequency is 10.4 kHz (±1.2 kHz), the terminal frequency is 7.0 (±1.4 kHz), and the peak-to-terminal frequency difference is 3.4 kHz (±1.0 kHz). "C chirps" are emitted in anticipation of feeding or during environmental exploration. The vocalizer exhibits a cautious approach to the target object, often with its mouth open. Other tamarins hearing this call seldom vocalize in response.

D chirps: These calls consist of a single syllable 42.6 ms (±10.2 ms) in duration, including a stem upsweep. The initial frequency is 7.7 kHz (±0.7 kHz), the peak frequency is 8.2 kHz (±0.7 kHz), the terminal frequency is 5.0 kHz (±1.4 kHz), and the peak-to-terminal frequency difference is 3.3 kHz (±1.5 kHz). "D chirps" are emitted when animals are begging for food or after it has been taken. The vocalizer, who can either be in motion or stationary, is usually in possession of food. Animals of all age classes approach the vocalizer and solicit food.

E chirps: These calls consist of a single syllable 36.9 ms (±10.4 ms) in duration,including a stem upsweep. The initial frequency is 6.4 kHz (±1.5 kHz), the peak frequency is 8.0 kHz (±1.6 kHz), the terminal frequency is 4.9 kHz (±1.5 kHz), and the peak-to-terminal frequency difference is 3.1 kHz (±1.2 kHz). "E chirps" are emitted during situations involving general alarm. The vocalizer often orients toward the sound source, showing moderate piloerection, and exhibits startle responses while performing rapid locomotor activity and scanning. Tamarins hearing this call sometime emit "E chirps" in response, often exhibiting startle responses and moderate piloerection while fleeing from the sound source. These calls can be encouraged by sudden visual or acoustic stimuli.

These are the most variable of the chirps, with their symmetry dependent on the emotional state of the animal. Mildly aroused animals emit "E chirps" featuring spectrographic profiles with an "inverted J" configuration, changing to an "inverted U" configuration in maximally aroused animals.

F chirps: These relatively short calls consist of a single syllable 53.0 ms (±19.7 ms) in duration and without a stem upsweep. The initial frequency is 4.1 kHz (±0.7 kHz), the peak frequency is 4.1 kHz (±0.7 kHz), the terminal frequency is 3.2 kHz (±0.7 kHz), and the peak-to-terminal frequency difference is 1.0 kHz (±0.4 kHz). "F chirps" function in short range intergroup vigilance and are often emitted antiphonally in response to the long calls of unfamiliar tamarins. The vocalizer often becomes stationary, shows moderate piloerection, and sometimes performs ceiling scans. Non-troop members hearing this call often emit "combination long calls" or "F chirps + whistle calls". Troop members hearing this call emit "F chirps" or fail to respond.

G chirps: These calls consist of a single syllable 57.9 ms (±10.7ms) in duration and possess no stem upsweep. The initial frequency is 9.0 kHz (±1.1 kHz), the peak frequency is 9.0 kHz (±1.1 kHz), the terminal frequency is 6.1 kHz (±0.9 kHz), and the peak-to-terminal frequency difference is 6.1 kHz (±0.7 kHz). "G chirps" are emitted during non-specific environmental investigations. The vocalizer appears to be relaxed and often tilts its head toward target objects. Tamarins hearing this call seldom respond.

H chirps: These calls consist of a single syllable 20.8 ms (±4.1 ms) in duration and possess no stem upsweep. The initial frequency is 5.5 kHz (±0.8 kHz), the peak frequency is 5.5 kHz (±0.8 kHz), the terminal frequency is 2.6 kHz (±0.7 kHz), and the peak-to-terminal frequency difference is 2.9 kHz (±0.8 kHz). "H chirps" are emitted under situations of low level arousal. The vocalizer often shows visual fixation on target objects as it approaches them, often slightly tilting its head, while showing minimal piloerection. Tamarins hearing this call often behave similarly to the vocalizer, including frequently emitting "H chirps."

The following calls each feature distinctly longer durations than the preceding chirps.

Squeals: These calls are 240 ms (±87.8 ms) in duration. The initial frequency is 6.9 kHz (±0.7 kHz) and the terminal frequency is 5.8 kHz (±0.7 kHz). Squeals are frequently emitted by immature animals or by those demonstrating submission to a dominant animal. They are often emitted by animals engaging in rough-and-tumble wrestling, especially if there is face pressing or if one animal attempts to terminate the bout. The vocalizer often displays crouching behaviors and hair flattening. Tamarins hearing these calls seldom respond.

Slicing screams: These calls are 340 ms (±95.8 ms) in duration. The initial frequency is 5.2 kHz (±1.4 kHz), the peak frequency is 7.9 kHz (±1.3 kHz), and the terminal frequency is 2.28 kHz (±0.3 kHz). Slicing screams are modified "A" chirps and are emitted during mobbing. Tamarins hearing these calls often participate in the mobbing while emitting "A chirps," "slicing screams," and "E chirp chatter".

Class Two Vocalizations: Pulsed Vocalizations

This class of vocalizations consists of twitters, chatters, and trills.

Twitters: These short calls never exceed 100 ms in duration and are essentially intensified squeals, emitted when animals are highly aroused (Epple, 1968). They are emitted during the same behavioral contexts as squeals, i.e., rough-and-tumble wrestling. The duration of twitters often corresponds to the duration of the wrestling bout.

With the exception of "chevron chatter," all of the following vocalizations are derived from class one vocalizations. Compared to the contexts within which their source vocalizations are employed, all of these calls are emitted under conditions of relatively high arousal.

Hooked chatter: These calls have a duration of 44.4 ms (±9.9 ms) with an emission rate of 6.1 (±1.3) units per second. The initial frequency is 7.8 kHz (±0.7 kHz), the peak frequency is 7.9 kHz (±0.7 kHz), and the terminal frequency is 4.2 kHz (±1.2 kHz). Hooked chatter consists of elements that resemble modified "D chirps," and as such are associated with food related situations. Hooked chatter is emitted at high rates and intensities with widely open mouths. The vocalizer is often an older animal in possession of food or a younger animal attempting to investigate a desirable object possessed by another animal.

Chevron chatter: These calls have a duration of 21.8 ms (±6.1 ms), with an emission rate of 1.4 (±1.5) units per second. The initial frequency is 3.3 kHz (±1.1 kHz), the peak frequency is 3.5 kHz (±0.9 kHz), and the terminal frequency is 2.1 kHz (±0.3 kHz). The vocalizer often shows piloerection, head shaking, tongue flicking, and evasive locomotion. Tamarins hearing these calls often respond with orientation toward the source, piloerection, "long calls," and "combination long calls". These calls are often emitted when animals are handled for routine veterinary procedures.

E chirp chatter: These calls are composed of a series of elements statistically indistinguishable from those forming "E chirps". "E chirp chatter" occurs during mobbing situations and under conditions of extreme arousal. The behavior of the vocalizer is similar to tamarins emitting "A chirps," while the behavior of respondents is similar to animals hearing "A chirps".

F chirp trills: These calls are composed of a series of elements statistically indistinguishable from those forming "F chirps". The behavior of the vocalizer is similar to that of tamarins emitting "F chirps," while the behavior of respondents is similar to that of animals hearing "F chirps," though the context usually involves elevated arousal. These calls are often emitted in response to "F chirps" or "F chirp trills," especially those of non-troop members.

H chirp trills: These calls are composed of a series of elements statistically indistinguishable from those forming "H chirps". The behavior of the vocalizer is similar to that of tamarins emitting "H chirps," while the behavior of respondents is similar to that of animals hearing "H chirps," though the context usually involves elevated arousal. "H chirp trills" often precede "H chirps" and are sometimes emitted in response to novel visual stimuli.

The following calls are not derived from class one vocalizations. All feature low amplitudes and minimal frequency modulation.

A trills: These calls are 38.8 ms (±9.1 ms) in duration with an emission rate of 10.9 (±2.0) units per second. The initial frequency is 4.4 kHz (±1.4 kHz), the peak frequency is 4.4 kHz (±1.4 kHz), and the terminal frequency is 2.7 kHz (±0.6 kHz). The vocalizer often slowly approaches other animals or sound sources while exhibiting head shaking and moderate piloerection. Tamarins hearing "A trills" show moderate piloerection, visual fixation on the sound source, and often emit "A trills," "initially modulated whistles," and "combination long calls". "A trills" are often emitted during and following antiphonal calling or immediately preceding bouts of play mounting.

B trills: These calls are 28.5 ms (±6.3 ms) in duration with an emission rate of 12.8 (±1.9) units per second. The initial frequency is 4.6 kHz (±1.1 kHz), the peak frequency is 4.6 kHz (±1.1 kHz), and the terminal frequency is 3.3 kHz (±0.9 kHz). The vocalizer often displays rapid head tilting, tongue flicking, and head or tail piloerection. "B trills" are emitted by adults as they approach infants, especially toward infants attempting to break contact with adults.

C trills: These calls are 24.4 ms (±5.5 ms) in duration with emission rates of 8.3 (±2.3) units per second. The initial frequency is 4.4 kHz (±0.6 kHz), the peak frequency is 4.4 kHz (±0.6 kHz), and the terminal frequency is 3.2 kHz (±0.5 kHz). "C trills" signal the beginning and ending of nursing bouts. They are often emitted by adult females toward infants when they are attempting to encourage or discourage nursing by pushing the head of the infant toward or away from their nipples. Occasionally "C trills" are interspersed with "terminally modulated whistles."

Class Three Vocalizations: Single Whistles

This class of vocalizations includes squeaks and single whistles. There are four slightly modulated vocalizations, distinguished by the position of the frequency modulation: "initially modulated whistle," "terminally modulated whistle," "flat whistle," and "squeaks". "Initially modulated whistles" feature maximum frequency modulation within the initial 100 ms of the call, while "terminally modulated whistles" feature maximum frequency modulation within the terminal 100 ms of the call. "Flat whistles" feature no frequency modulation and are distinguished from squeaks by their longer duration and higher initial and terminal frequencies. All four vocalizations occur under conditions of minimal arousal, although "squeaks" can occur within any context except undisturbed rest.

Small, initially modulated single whistles: These calls are 495.8 ms (±106 ms) in duration. The initial frequency is 3.7 kHz (± 1.1 kHz), the peak frequency is 3.8 kHz (±1.1 kHz), and the terminal frequency is 2.9 kHz (±0.3 kHz). Small, initially modulated single whistles are contact calls emitted at distances of less than 0.6 meters, often by animals sitting together engaging in low level vigilance. The vocalizer is usually stationary, often displaying a slightly open mouth. These calls are often emitted during antiphonal calling, hence, respondents often emit the same call.

Large, initially modulated single whistles: These calls are 566.2 ms (±96.1 ms) in duration. The initial frequency is 6.3 kHz (± 1.6 kHz), the peak frequency is 6.5 kHz (±1.6 kHz), and the terminal frequency is 2.7 kHz (±0.3 kHz). Large initially modulated single whistles are contact calls emitted by animals at distances greater than 0.6 m from one another. The primary structural difference between this and the preceding call is the greater amount of frequency modulation in the "large initially modulated single whistle," providing additional cues to location when animals are not in visual contact. They are also functionally similar to the preceding call, though they are sometimes emitted when animals terminate contact.

Terminally modulated whistles: These calls are 465.9 ms (±82.6 ms) in duration. The initial frequency is 2.1 kHz (±0.6 kHz), the peak frequency is 2.1 kHz (±0.6 kHz), and the terminal frequency is 2.5 kHz (±0.4 kHz). Terminally modulated whistles are usually emitted by relaxed animals, often a mother nursing or retrieving an infant. The vocalizer is usually stationary, displaying a slightly open mouth. Other tamarins often fail to respond to these vocalizations.

Flat whistles: These calls are 326 ms (±97.5 ms) in duration. The initial frequency is 2.2 kHz (±0.6 kHz), the peak frequency is 2.2 kHz (±.6 kHz), and the terminal frequency is 2.5 kHz (±0.5 kHz). Flat whistles are emitted when tamarins are highly aroused, often in response to type "E chirp trills," "B chirp trills," or "H chirp trills". The vocalizer often exhibits visual fixation on sound sources, displays moderate piloerection, and performs scanning. Sometimes, the vocalizer also emits "F chirps" and "H chirp trills" interspersed with "flat whistles". Other tamarins often fail to respond to these vocalizations.

Squeaks: These calls are 99.3 ms (±32.5 ms) in duration. The initial frequency is 3.0 kHz (±0.2 kHz), while the terminal frequency is 3.1 kHz (±0.3 kHz). Squeaks are emitted during foraging and environmental exploration. The vocalizer displays moderate arousal through rapid locomotion and piloerection. The rate of emission of squeaks increases as levels of arousal rise.

Class Four: Multiwhistles

Multiwhistles are composed of a series of individual whistle units forming phrases. This class of calls functions in intergroup spatial regulation and intratroop cohesion. Although there is some functional overlap, the calls are structurally distinct.

The following vocalizations are important in intratroop cohesion:

Ascending multiwhistles: This call consists of two segments. The first segment is 172 ms (±36.9 ms) in duration. The initial frequency is 2.1 kHz (±0.3 kHz), while the terminal frequency is 2.4 kHz (±0.4 kHz). The second segment is 145.4 ms (±32.5 ms) in duration. The initial frequency is 2.4 kHz (±0.4 kHz) while the terminal frequency is 2.7 kHz (±0.4 kHz). Ascending multiwhistles are emitted during situations of affiliation and relaxation, often by mothers with infants or by animals huddling together. Vocalizers often lie on their sides with tails coiled over their abdomens. Other tamarins often fail to respond to these calls.

Descending multiwhistles: These calls consist of three segments. The first is 169.2 ms (±37 ms) in duration. The initial frequency is 2.4 kHz (±0.6 kHz), while the terminal frequency is 2.3 kHz (±0.5 kHz). The second segment is 163.5 ms (±26.2 ms) in duration. The initial frequency is 2.0 kHz (±0.5 kHz), while the terminal frequency is 2.2 kHz (±0.4 kHz). The third segment is 146.1 ms

(±55.7 ms) in duration. The initial frequency is 2.2 kHz (±0.6 kHz), while the terminal frequency is 2.5 kHz (±0.5 kHz). "Descending multiwhistles" are emitted during situations of affiliation and relaxation, often by adults toward infants. Respondents sometimes exhibit head shaking or tongue flicking while orienting toward the sound source. "Descending multiwhistles" are sometimes interspersed with "terminally modulated whistles". Other tamarins often fail to respond to these vocalizations.

Partial quiet long calls: These calls consist of two segments. The first is 239.3 ms (±109.8 ms) in duration. The initial frequency is 1.8 kHz (±0.5 kHz), while the terminal frequency is 1.7 kHz (±0.4 kHz). The second segment is 435.7 ms (±127.3 ms) in duration. The initial frequency is 1.15 kHz (±0.3 kHz), while the terminal frequency is 2.4 kHz (±0.3 kHz). "Partial quiet long calls" are multilevel whistles important in intratroop cohesion. They are often emitted by mothers with infants. Vocalizers are usually stationary and appear relaxed. Other tamarins often fail to respond to these vocalizations.

The following vocalizations are important in intergroup spatial regulation.

Quiet long calls: These calls consist of three segments. The first is 266.0 ms (±72.4 ms) in duration. The initial frequency is 1.2 kHz (±0.6 kHz), while the terminal frequency is 1.1 kHz (±0.4 kHz). The second segment is 525.0 ms (±210.7 ms) in duration. The initial frequency is 1.2 kHz (±0.4 kHz), while the terminal frequency is 1.5 kHz (±0.2 kHz). The third segment is 725.7 ms (±258.7 ms) in duration. The initial frequency is 1.2 kHz (±0.3 kHz), while the terminal frequency is 2.2 kHz (±0.4 kHz). "Quiet long calls" are often emitted in response to the single whistles or long calls of unfamiliar animals. Vocalizers often exhibit slow forward locomotion, moderate piloerection, and rapid scanning. These calls are usually emitted by more than one animal simultaneously. If respondents are nontroop members, they emit "quiet long calls," especially if they are close to the sound source, or "normal long calls" if they are more distant from it. Respondents belonging to the troop emit overlapping "quiet long calls" antiphonally.

Normal long calls: These calls consist of three segments. The first is 223.4 ms (±79.7 ms) in duration. The initial frequency is 1.6 kHz (±0.6 kHz), while the terminal frequency is 1.1 kHz (±0.3 kHz). The second segment is 1132.0 ms (±173.1 ms) in duration. The initial frequency is 1.0 (±0.2 kHz), while the terminal frequency is 1.2 kHz (±0.2 kHz). The third segment is 1079.0 ms (±208.8 ms) in duration. The initial frequency is 1.1 kHz (±0.2 kHz), while the terminal frequency is 1.5 kHz (±0.2 kHz). "Normal long calls" are important in intergroup spatial regulation. Vocalizers often assume a stationary position, display moderate piloerection, perform continuous scanning, and vocalize with widely open mouths. Nongroup respondents often emit nonoverlapping "normal long calls" antiphonally. Respondents belonging to the group seldom emit vocalizations, but adopt stationary, vigilant stances and perform rapid scanning.

Class Five: Combination Vocalizations

All of these vocalizations consist of phrases formed of whistles preceded by variable numbers of chirp units, and include the following: multilevel whistles, combination long calls, inverted U + whistles, and F chirp + whistles. Three of these calls feature introductory chirps preceding the whistle segment. The two variants of the "multilevel whistle" differ in peak frequency and degree of frequency modulation of the stem upsweep within the initial chirp unit. The "combination long call" is the single most variable vocalization within the entire repertoire.

Large modulation multilevel whistles: This call consists of several chirp units and two whistle segments. The initial chirp unit is 130.3 ms (±36.0 ms) in duration with a mean emission rate of 2.8 units per second. The initial frequency is 5.6 kHz (±1.3 kHz), the peak frequency is 5.7 kHz (±1.2 kHz), and the terminal frequency is 3.2 kHz (±0.6 kHz). The initial whistle unit is 148.7 ms (±28.0 ms) in duration. The initial frequency is 2.7 kHz (±0.4 kHz), while the terminal frequency is 2.7 kHz (±0.4 kHz). The terminal whistle unit is 225.6 ms (±89.3 ms) in duration. The initial frequency is 2.8 kHz (±0.4 kHz), while the terminal frequency is 2.8 kHz (±0.4 kHz). Although structurally distinct, the social contexts, vocalizer behavior, and respondent behavior are similar for both the "large modulation multilevel whistle" and the "small, initially modulated whistle".

Small modulation multilevel whistles: This call consists of one chirp unit and a single whistle element. The chirp is 137.1 ms (± 24.3 ms) in duration, with a mean emission rate of 2.3 units per second. The initial frequency is 4.6 kHz (±1.3 kHz), the peak frequency is 4.7 kHz (±1.3 kHz), and the terminal frequency is 3.3 kHz (±0.3 kHz). The whistle segment is 229.2 ms (±89.3 ms) in duration. The initial frequency is 2.9 kHz (±0.3 kHz), while the terminal frequency is 3.0 kHz (±0.2 kHz). Although structurally distinct, the social contexts, vocalizer behavior, and respondent behavior are similar for both the "small modulation multilevel whistle" and the "small, initially modulated whistle".

Combination long calls: This call consists of four elements: initial and terminal chirp elements and initial and terminal whistle segments. The initial chirp has a peak frequency of 8.1 kHz (±1.4 kHz), while the terminal chirp unit has a peak frequency of 3.3 kHz (±1.1 kHz). The initial whistle unit is 338.2 ms (±105.9 ms) in duration. The initial frequency is 2.0 kHz (±0.5 kHz), while the terminal frequency is 1.9 kHz (±0.4 kHz). The terminal whistle unit is 401.3 ms (±147.9 ms) in duration. The initial frequency is 1.8 kHz (±0.4 kHz), while the terminal frequency is 2.0 kHz (±0.4 kHz). The "combination long call" is the most variable vocalization within this repertoire. It is emitted during situations of elevated arousal, including during play bouts, mobbing situations, cage cleaning procedures, or when animals are newly paired. The call might also function as a type of "lost call" emitted by troop members to provide locational cues to animals out of visual contact with the group. Vocalizers often display rapid, erratic locomotion, scanning, piloerection, and continuous vocalizing. Respondents often emit "combination long calls" or "normal long calls" antiphonally. "Combination long calls" are sometimes emitted in response to the "normal long calls" of unfamiliar tamarins.

Inverted U + whistles: This call consists of a single chirp unit and a whistle segment. The chirp unit is 50.7 ms (±23.3 ms) in duration. The initial frequency is 4.6 kHz (±0.7 kHz), the peak frequency is 5.8 kHz (±0.9 kHz), and the terminal frequency is 4.4 kHz (±0.6 kHz). The whistle segment is 108.3 ms (±33.0 ms) in duration. The initial frequency is 3.6 kHz (±0.3 kHz), while the terminal frequency is 3.7 kHz (±0.3 kHz). "Inverted U + whistles" are emitted in response to the alarm vocalizations of other troop members. The vocalizer often becomes stationary, scans the top of its enclosure, shows moderate piloerection, and vocalizes--often emitting the same call. Respondents behave similarly to the vocalizer.

Type F chirp + whistles: This call consists of a single chirp unit and three whistle segments. The chirp is 73.1 ms (±23.2 ms) in duration. The initial frequency is 4.2 kHz (±0.8 kHz), the peak frequency is 4.2 kHz (±0.8 kHz), and the terminal frequency is 3.0 kHz (±0.5 kHz). The initial whistle segment is 332.7 ms (±104.7 ms) in duration. The initial frequency is 2.1 kHz (±0.4 kHz), while the terminal frequency is 1.7 kHz (±0.3 kHz). The second whistle segment is 476.9 ms (±71.0 ms) in duration. The initial frequency is 1.5 kHz (±0.2

kHz), while the terminal frequency is 1.6 kHz (±0.3 kHz). The terminal whistle unit is 530.8 ms (±109.2 ms) in duration. The initial frequency is 1.5 kHz (±0.2 kHz), while the terminal frequency is 1.8 kHz (±0.2 kHz). Although structurally distinct, the social contexts, vocalizer behavior, and respondent behavior are similar for both the "F chirp + whistle" and the "normal long call," although the vocalizer occasionally displays an increase in the intensity of erratic locomotor behavior. "F chirp + whistles" are often emitted by subordinate animals or others in response to "normal long calls" or "combination long calls." Respondents often orient toward the source of the vocalizations, show piloerection, and emit "normal long calls".

Class Six: Noisy Vocalizations

All of these calls feature wide energy distributions, minimal tonal aspects, and many inharmonic qualities. They include squawks, screams, and sneezes.

Squawks: These calls range in duration from 100 ms to 3450 ms, with an average duration of 300 ms. Most of the energy is concentrated below 7.0 kHz. The calls feature sharp rise times and variable tonal qualities. The tonal quality of the call is altered by the degree to which the mouth is open. Squawks are emitted during wrestling with face pressing, when animals are slapped, or during role reversals within grooming bouts. Occasionally, it is emitted by animals soliciting grooming. The intensity and rate of emission of squawks depends on the vocalizer's degree of arousal. Vocalizers often display evasive locomotor behavior and crouching. Other tamarins seldom display overt responses to these vocalizations.

Screams: These calls are emitted by animals performing evasive locomotor behavior, often in possession of food. Occasionally the vocalizer salivates or performs head shaking. They are infrequently emitted, and other tamarins seldom respond to them.

Sneezes: These sounds are always under 400 ms in duration. They are emitted explosively, with their maximum energy below 5.0 kHz. Sneezes are functionally equivalent to those observed in other mammals. Tamarins often sneeze after feeding, drinking, or sniffing objects.

Screams appear to be derived from the combination of squawks with several extremely variable atonal units.

The vocal repertoire of the cotton-top tamarin is based on only 13 primary elements, five whistles and eight chirps, yet the number of discrete signals is increased by their recombination. Tamarins often emit structurally similar vocalizations varying only slightly in one parameter to convey specific messages within different social contexts. This is similar to the profound changes in perceptual categorization that occur in human speech through very slight alterations in morphemes or phonemes. For example, a slight retardation of 10 ms in the stop plosive /t/ in "at" produces the /d/ in "ad." The crucial difference between these phonemes is the presence of different voicings.

The meaning of vocalizations can be changed to accommodate different social settings through increases in emission rate, intensity, or duration, all of which correlate with changes in the emotional state of the animal.

The intensity of a call can be increased through its repetition. For example, "chatters," "trills," and "twitters" all feature repeated "chirp" units and reflect greater levels of arousal than individual chirps. Several trills, including "A trills," "B trills," and "C trills" are emitted within disquieted social contexts, situations within which vocal behavior characteristic of minimal arousal, e.g., antiphonal calling with "long whistles," seldom occurs.

Other whistles can be emitted during disquieted situations, when they are repeated to reflect more intense social contexts. Long calls, for example, are derived from single whistle units, reflecting intensified interactions. Several long call variants, including "quiet long calls," "normal long calls," and "combination long calls" are emitted in intense interactions, where, at reduced intensities, "single whistles" would be emitted.

Affiliation calls, including the "terminally modulated whistle," "ascending multi-level whistle," and the "partial quiet long call" exhibit increases in modal frequency across their respective durations. This characteristic precisely matches the predictions of Morton (1977), which state that appeasement vocalizations should increase in frequency throughout their durations.

Alarm calls, including "A chirps," "E chirps," and "chevron chatter" feature chevron-shaped spectrographic profiles, again, as predicted by Morton (1977). Further, their wide energy distributions and resulting subjective harshness also match these predictions.

Harsh sounding vocalizations are correlated with elevated arousal, agonism, and potential aggression. Epple (1968) confirms that callitrichids emit "squawks" and "screams" during agonistic encounters.

The prediction that harsh sounding vocalizations are strictly associated with intense social situations is disconfirmed by the emission of "squawks" preceding grooming sessions in Geoffroy's tamarins (Moynihan, 1970) and saddleback tamarins (Moody & Menzel, 1976).

The changes in morphology that correlate with intensity are exemplified by the distinctly different spectrograms derived from vocalizations emitted during intense and quiet interactions. The "B chirp" is emitted during nondirected investigatory behavior, the "C chirp" and "D chirp" in association with feeding, and the "F chirp" in low level intergroup interactions. Their spectrograms feature "inverted J" configurations resulting from unequal stem upsweeps and downsweeps. The "A chirp" is emitted during mobbing, the "E chirp" under general alarm, and "chevron chatter" when animals are highly aroused. Their spectrograms feature "inverted U" configurations resulting from equivalent stem upsweeps and downsweeps. The morphological changes in call structure that correlate with elevated emotional intensity include increased call duration, increased frequency modulation, and an elongation of the stem downsweep, producing the chevron shaped profile associated with situational urgency.

Some calls feature morphologies indicative of conflicting motivational tendencies. "A chirps" are most frequently associated with mobbing situations. Animals engaging in mobbing perform behaviors suggesting that their is a simultaneous urge to flee from an aversive situation and to mob an intruder. Morton (1977) suggests that vocalizations associated with increased fear should exhibit long durations or that single element vocalizations should be repeated to produce vocalizations indicative of elevated arousal, e.g., "chatters," "trills," or "twitters." Hence, when animals are aroused, they emit "A chirps," which feature relatively long durations, and "E chirp chatter," which is derived from "E chirps," typically emitted during less intense situations. Cotton-top tamarins emit variants of single frequency modulated calls within specific contexts, i.e., all chirps are situationally distinct. For example, "A chirps" are associated with mobbing, "C chirps" are emitted immediately preceding feeding, "D chirps" are emitted after feeding, "E chirps represent general alarm, and "H chirps" are emitted in response to novel visual stimuli. Single whistles are less easily correlated with specific contexts.

The degree to which this repertoire resembles those of other tamarins is difficult to assess. Various researchers employ different classification schemes and technologies. Recent research, which benefits from technological advances, tends to describe larger repertoires than earlier research. Consequently, direct comparisons between the repertoires of the cotton-top tamarin and that of the Geoffroy's tamarin, based on earlier research, should be approached cautiously.

The requirement for such a comparison arises from the use of recordings of vocalizations from both cotton-top tamarins and Geoffroy's tamarins in this research. Whether or not tamarins representing either subspecies are differentially responsive to vocalizations from conspecifics versus congeners is not clear. Both species appear to employ "trill-like" and "twitter-like" calls in similar situations. Although subjectively similar, the structural equivalency of these calls has not been established. Whether or not the "initial sharp trill element" emitted by Geoffroy's tamarins to sudden stimuli (Moynihan, 1970) is functionally equivalent to the various alarm calls of the cotton-top tamarin also remains unclear. Similar uncertainty extends to the "long whistles" of Geoffroy's tamarins and the "quiet long calls" of cotton-top tamarins, the "quiet whistles" of Geoffroy's tamarins and the "quiet long calls" of cotton-top tamarins, and, finally, the "grunts" and "barks" of Geoffroy's tamarins and the "squeaks" and "squawks" of cotton-top tamarins (Cleveland & Snowdon, 1982; Moynihan, 1970). Obviously, considerably more research needs to be conducted to resolve these questions.

Within the genus, however, animals representing different species appear to respond to the calls of congeners. Sympatric mustache tamarins, emperor tamarins, and saddleback tamarins respond to interspecific vocalizations during foraging (Terborgh, 1983). Sympatric subspecies of saddleback tamarins respond to the vocalizations of individuals of other subspecies (Hodun, Snowdon, & Soini, 1981). Cotton-top tamarins and Geoffroy's tamarins also appear to respond to one another's vocalizations (Epple, 1968). These findings suggest that the high degree of vocal convergence within the taxon facilitates congeneric responsiveness to many classes of vocalizations.

The following vocal repertoire is presented to describe the vocalizations that were included in some of the playback treatments featuring recordings of free-living Geoffroy's tamarins.

Synopsis of the Vocal Repertoire of Geoffroy's Tamarin

The vocal repertoire proposed for Geoffroy's tamarin (Moynihan, 1970), is based on much earlier research than that proposed for the cotton-top tamarin (Cleveland & Snowdon, 1982), and is smaller, less complete, less quantitative, and more subjective. Vocalizations are variously described as "chirps," "rasps," "squeaks," "squeals," "trills," "twitters," "whines," and "whistles". Many vocalizations are described as being composed of rapidly emitted sequences of discrete units. However, since the data were obtained from the field, the precise structures of vocalizations can be difficult to assess. Consequently, many calls described as being composed of single units are probably composed of several sub-units, termed "notes" by Moynihan (1970).

The following repertoire is derived from the work of Moynihan, (1970) and is based on structure, irrespective of function. The hierarchical organization present in the repertoire proposed for the cotton-top tamarin (Cleveland & Snowdon, 1982) is not present, hence the absence of classes. The repertoire consists of "barks," "chatters," "chirps," "grunts," "long whistles," "rasps," "screams," "screeches," "short alarm calls," "squeaks," "squeals," "trills," "twitters," "whines," and "whistles".

A chirps: These vocalizations, sometimes termed "tsee calls" (Epple, 1968; Moynihan, 1970), are short in duration and high pitched, ranging between 1.5 kHz and 2.5 kHz. "A chirps" function as contact calls and are emitted by relaxed animals in visual contact with one another.

B chirps: These vocalizations are short in duration and high pitched, ranging between 2.5 kHz and 4.0 kHz. Their intensities, durations, frequencies, and degrees of modulation are extremely variable. "B chirps" function as isolation calls and are emitted by animals when they are not in secure visual contact with other troop members.

Trills: These vocalizations consist of from 2 to 25 intense elements, each featuring a rapid onset. The initial elements exhibit a decrease in fundamental frequency across their duration. The terminal elements also exhibit a rapid onset and decrease in fundamental frequency throughout their durations. These calls show considerable energy between 16 kHz and 45 kHz (Epple, 1968). The structure of trills is extremely variable and often difficult to distinguish from "twitters". Moynihan (1970) contends that the fundamental frequency of "trills" increases with the arousal level of the vocalizer. Trills often consist of a single, intense initial "trill" element combined with "twitters". "Trills" function in several contexts, including alarm, mobbing, and when troop members lose visual contact with the group.

They are emitted in the same situations as "whines," usually in response to the sight of large mammals, aerial predators, and caretakers. Motivationally, "trills" are correlated with tendencies to escape. A short, intense initial "trill" element with considerable acoustic energy at 45 kHz is emitted in response to the presence of potential predators and appears to function as an alarm call. These calls are infectious and spread rapidly throughout a troop. Another vocalization, structurally similar to the alarm call except for its lower amplitude, is employed in intratroop interactions, primarily those associated with feeding and grooming. These are emitted under conditions of minimal arousal and function as close range cohesion calls.

Twitters: These vocalizations consist of from four to seven short, high pitched units. Twitters function as low intensity responses to potentially arousing stimuli. They are often emitted in response to the presence of neutral animals or potential predators and in response to the alarm calls of other tamarins. Respondents often emit mobbing or alarm calls while exhibiting mobbing behavior.

Captive tamarins often emit twitters in response to the presence of familiar caretakers. The emission of "twitters" in affiliative interactions is thought to represent a form of infantile vocal behavior and is most frequently observed in tamed animals (Epple, 1968; Moynihan, 1970).

Elongation of individual "twitter" elements forms "long whistles". These derived calls also function in affiliative interactions and are often emitted by animals engaging in play behavior.

Squeals: These vocalizations are frequently emitted by young animals and by adults submitting to dominant troop members. Captive tamarins emit more infantile type vocalizations, including squeals, than wild tamarins (Epple, 1975).

A trills: These vocalizations consist of sequences of short, rapidly emitted units. Their energy is widely distributed, with considerable energy present at 24.0 kHz. "A trills" are emitted in response to the presence of potential predators. Tamarins hearing "A trills" emit the same call, which often spreads throughout a troop.

Chatters: These vocalizations are emitted during situations involving defensive threat.

Short syllable mobbing calls: These vocalizations, sometimes termed "tsik calls," range in frequency from 2.0 kHz to 6.0 kHz. The fundamental frequency increases with the vocalizer's level of arousal. Though structurally distinct, "short syllable mobbing calls" are contextually similar to "trills" and are often emitted in conjunction with them.

Long whistles: These vocalizations consist of from two to four segments combined into a single call. The energy distribution is wide, with the amplitudes of the second, third, and fourth harmonics almost equivalent to that of the fundamental frequency. "Long whistles" are described as plaintive sounding by Moynihan (1970). Long whistles function in territorial defense, long distance communication with other troop members, as "lost calls" for separated troop members, and in reproduction. Single animals often emit "long whistles" to attract mates. The calls might also be important in the formation and maintenance of pair bonds.

Rasps and Screeches: These vocalizations consist of rapidly emitted pulses of energy, increasing in fundamental frequency throughout the duration of the call. Rasps can be continuous, "long rasps," or discontinuous, "broken rasps". They function in situations of intraspecific aggression and are often emitted by animals engaging in chasing and wrestling.

Screams: These vocalizations are high intensity calls often emitted by infants in distress or by juveniles expressing agonism.

Grunts and Barks: These vocalizations are short, low frequency calls emitted exclusively during agonistic encounters.

Whines: These are moderately short vocalizations often emitted by animals separated from their troops. They are especially frequent in captive settings. "Whines" with slightly shorter durations are sometimes emitted by animals indicating low levels of potential hostility. Other tamarins respond to "whines" with elevated levels of scanning, "long whistles," or the same call.

The absence of spectrographic corroboration and incomplete descriptions of the preceding calls require that proposed functional equivalencies be determined through comparisons of behavioral contexts. This task is complicated by idiosyncratic classifications and onomatopoeic descriptions. Nonetheless, the research of Epple (1968), Moynihan (1970), and Cleveland and Snowdon (1982) feature sufficient homologies and analogies to invite discussion.

The vocalizations of all Callitrichids are often described as high pitched whistles and chirps, "flute-like," and "bird-like" (Epple, 1968; Hershkovitz, 1977; Moynihan, 1970; 1976). There is remarkable convergence in structure across the taxon. The high degree of morphological similarity of Callitrichid vocalizations is in part an artifact of their close taxonomic affinities (Hershkovitz, 1977), in part the result of adaptations to similar acoustic habitats (Waser & Brown, 1986; Wiley & Richards, 1978), and in part from similar motivational influences on vocal morphology and behavior (Morton, 1975; 1977). Finally, call morphology is influenced by distinct local traditions, often involving the evolution of dialects (Smith, 1981; Snowdon, 1985). All species possess highly discrete, categorical repertoires--well adapted to forest habitats. The influence of artificial habitats on the development of these vocal repertoires is not presently clear.

Captive cotton-top tamarins and Geoffroy's tamarins are reported to vocalize more frequently than other Callitrichids (Epple, 1968), while wild cotton-top tamarins are reported to vocalize relatively infrequently (Neyman, 1978). Moynihan (1970) reports that captive Geoffroy's tamarins emit variable vocalizations in response to changes in their enclosures. Similarly, Epple (1968) reports that captive cotton-top tamarins respond to changes in their enclosures with several types of monosyllabic vocalizations. Environmental changes, including the introduction of mildly distressing stimuli, the presence of other animals--including potential predators--or the disruption of visual contact with conspecifics stimulates vocalization in each species. Captive tamarins appear to emit more juvenile vocalizations than their wild counterparts (Moynihan, 1970). Finally, stress, often elevated in captive primates, can influence vocal behavior. Highly aroused squirrel monkeys show variability in vocal behavior and morphology compared to less aroused animals (Joseph & Wilson, 1978). Thus, research on vocal behavior conducted in captive settings must be carefully monitored to reduce extraneous sources of stress on subjects to minimize its potential influence on vocal behavior.

The cotton-top tamarin and Geoffroy's tamarin appear to demonstrate the greatest variability in vocal morphology and behavior of any of the Callitrichids (Epple, 1968). Their vocal repertoires are complex communication systems, featuring large vocabularies, grammatical rules, and examples of syntactical organization. As research into the communication systems of the *Callitrichidae* continues apparently greater complexity is revealed. Because of their decline in the wild, much future research will be conducted in artificial settings. Consequently, the influence of captivity on the acoustic and vocal behavior of these and other primates must be investigated. Further, the influence of the acoustic habitat on other behaviors, including reproductive behaviors, must be more fully understood. This is especially critical as an increasing proportion of the remaining Callitrichids are found in zoos and laboratories, with their unnatural acoustic characteristics.

Conservation Status of the Callitrichidae

The destruction of natural habitats is increasing exponentially. While there are at least ten million species of plants and animals presently extant, fewer than 8.5 million of these have been identified. Unfortunately, over 40% of the tropical rain forests, in which most of this diversity exists, will be destroyed by the year 2000 (Myers, 1987). By the year 2030, the human population will reach approximately ten billion. At the same time, from one and one half to two million species of plants and animals existing today will have become extinct. As of 1985, at least one species a day was becoming extinct in the wild; by the year 2000 this rate will have risen to 24 species each day (Carpenter, 1983). Most of this destruction results from anthropogenic factors. The largest species (the charismatic megafauna), species with limited distributions, and those with easily disrupted social systems are the most vulnerable.

Among the most threatened groups of species are the neotropical primates, including virtually all Callitrichids (Marsh, Johns, & Ayres, 1987). Callitrichids inhabit disappearing primary forests, exhibit limited distributions, are relatively monogamous, produce relatively few young, are easily trapped, and have commercial value--a particularly unfortunate suite of attributes.

Due to the paucity of research on neotropical primates, their ecological role has only recently begun to be understood (Sussman & Kinzey, 1984). Primates are an integral part of the maintenance of homeostasis within tropical forest habitats, primarily because of their role in forest regeneration through seed dispersal (Bourlier, 1985; Garber, 1984b). Further, primates are a primary source of food for top-level carnivores. Consequently, the maintenance of adequate populations of primates in the wild has implications for the long term survival of other taxa. One type of pressure on wild primate populations that should be addressed is the capture of animals for use in research and entertainment. If the inconsistent reproduction and survival of neotropical primates could be improved in captivity, then replacement individuals could be recruited from sources other than nature, reducing one source of pressure on declining natural populations.

Gay (1986) has discussed the differential rate of breeding success within the family *Callitrichidae*. The common marmoset and the saddleback tamarin have proven to be relatively hardy animals in captivity (Stevenson, 1986), while cotton-top tamarins and the three subspecies of golden lion tamarins are considered to be the most endangered Callitrichids and have proven difficult to breed consistently in captivity (Kleiman, 1978; Mallinson, 1984).

Due to the critical conservation status of many Callitrichids, several strategies have been developed to attempt to preserve the remaining animals and their habitats.

Several national and international organizations and agencies have sought to regulate the exploitation of non-human primates and other animals, especially those threatened with imminent extinction. Some of these agencies administer laws and regulations governing the housing and maintenance of captive animals. These include the United States Department of Health and Human Services, which regulates importation of animals under title 42 (U.S.C. 264); the United States Department of the Interior, which administers the Endangered Species Act under title 16 (U.S.C. 1531-1543); and the United States Department of Agriculture, which administers animal housing regulations under title 7 (U.S.C.2131-2156). Additionally, there are international conventions that attempt to regulate commerce in endangered species and products made from them, e.g. the Convention on International Trade in Endangered Species (CITES) of Wild Fauna and Flora.

The cotton-top tamarin is listed under Appendix I of the CITES convention and is also listed as endangered under the United States Endangered Species Act (90-135-1977). So too is Geoffroy's tamarin which is the species most often trapped for the pet and biomedical trade (Mittermier, 1987). Further, both species have been listed in the Red Data Book of the International Union for the Conservation of Nature (IUCN) since 1973 (Mittermeier, Coimbra-Filho, & van Roosmalen, 1978).

The management of captive populations of endangered species has led to the development of stud books, an International Species Inventory System (ISIS), and species survival plans (SSP) (Carpenter, 1983; Conway, 1974). The introduction of these schemes closely parallels the changing role of the zoo from one emphasizing the consumption of animals to one that emphasizes their production and protection.

As with most neotropical primates, cotton-top tamarins are experiencing a rapid constriction in available habitat, and numbers of all three sub-species of *Saguinus oedipus* continue to decline in the wild (Marsh, Johns, Ayres, 1987; Mittermeier, 1986).

Most tamarins are too small to be considered efficient sources of protein and are not usually hunted for food. However, Geoffrey's tamarin is extensively hunted in Panama primarily due to its propensity for invading agricultural areas. It also offers a ready target for sport shooting (Dawson, 1978; Hershkovitz, 1977). Tamarins are also trapped for the biomedical trade, pet trade, and the exhibition trade (Kavanaugh, Eudey, & Mack, 1987). Young Geoffroy's tamarins are the most commonly captured Callitrichid to be sold illegally on the international market as pets (Moynihan, 1976). Cotton-top tamarins are also found on the illegal pet market, but less frequently so (Kleiman, 1978). Some rural Colombian families, however, occasionally keep them as pets (Neyman, 1978).

Over the past 25 years, cotton-top tamarins have become important medical models for the study of human oncoviruses and colonic disorders. During the peak years of the trade in primates, especially during the 1960's and 1970's, from 20,000 to 40,000 cotton-top tamarins were exported annually from Colombia to research institutions in the United States alone. Between 1968 and 1973, the year that several regulatory agreements went into effect, over 13,879 tamarins--2,800 of them cotton-top tamarins--were imported into the United States. Far more animals were trapped than survived to reach their intended destinations.

Throughout the 1960's, the mortality rate of wild caught tamarins shipped to the United States ranged between 25% and 32%, often reaching 80%. In 1972, the mortality rate for all Callitrichids approached 30%. Of 28,572 animals imported into the United States in 1978, 5,204 arrived at the port of entry dead, representing 18% of the original shipment. By 1979, the mortality rate had declined to 17%. Of over 22,700 animals, 2,808 were dead on arrival (Mittermeier, 1987; Wolffheim, 1983). As of 1985, cotton-top tamarins were thought to be virtually extinct in their former range. Even still, during the same year, immature cotton-top tamarins and Geoffroy's tamarins could be purchased in Panama (Merritt, 1986). Fortunately, the reproductive success of cotton-top tamarins in captivity is improving.

Between 1971 and 1980, over 776 animals were born in North American zoos. Unfortunately, over 41% of these animals died prematurely (Lindburg, *et al.*, 1986). As of 1990, over 1,800 cotton-top tamarins were registered with the appropriate agencies (Snowdon, 1990). Unfortunately, this is probably more than remain in the wild, where the pressure on vulnerable Callitrichid populations persists.

As important as live trapping is in reducing the numbers of these animals in the wild, it is not the only factor leading to their decline. Habitat disturbances resulting from primitive slash-and-burn agricultural practices and even from more modern selective logging are reducing the range available to both forms of *Saguinus oedipus*. The precise disposition of their populations in their native habitats is not entirely clear. While there have been several field studies on Geoffrey's tamarin (Dawson, 1978; Garber, 1984a), only one comprehensive study of the cotton-top tamarin has been conducted in the wild (Neyman, 1978). Geoffroy's tamarin is considered locally abundant in Panama (Moynihan, 1970), while the cotton-top tamarin is considered rare in Colombia.

Geoffroy's tamarins survive well in disturbed, secondary forest habitats (Dawson, 1978). This propensity for occupying disturbed habitats enables it to colonize areas which have been altered by agriculture. Increasingly, Geoffrey's tamarin has been able to invade and colonize abandoned agricultural fields and has become a commensal of humans along the Pacific coast of Panama (Moynihan, 1970; 1976; Wolfheim, 1983). Cotton-top tamarins do not coexist well with civilization, and apparently require large tracts of undisturbed mature rain forest in order to thrive (Myers, 1987).

Unfortunately, this habitat is quickly disappearing.

In northern Colombia, there are only 600 hectares of primary forest suitable for cotton-top tamarins remaining (Kleiman, 1978). This represents less than 5% of the original forest habitat of the Colombian tamarin (Wolfheim, 1983). Even this modest remnant, in the northeastern segment of the remaining range, consists of approximately 270 discontinuous patches of forest. Habitat is still being lost to logging for fence posts and conversion to pasture for the grazing of cattle (Myers, 1987).

The only population of Geoffrey's tamarain that exists in a protected area is on Barro Colorado Island, off of the coast of Panama. The cotton-top tamarin does not inhabit any reserve that is secure, since Colombian law encourages the expropriation of unexploited land by colonists. Geoffrey's tamarin is not protected in Panama, although commercial trapping and resale are regulated by the Panamanian Departments of Treasury and Natural Resources. In 1969 Colombia forbade the hunting and collection of cotton-top tamarins but in 1972 relaxed these regulations and allowed commercial collection to resume. As late as 1973, these regulations allowed for the taking of 100 animals per month in northern Colombia (Mittermeier, Coimbra-Filho, & van Roosmalen, 1978).

The remaining discontinuous patches of habitat often feature reduced resource diversity and, especially if resources are only seasonally available, are unable to support the remaining populations of tamarins (Happell, Moss, & Marsh, 1987). Ironically, the remaining islands of tamarin habitat resemble, and therefore can be managed like, naturalistic zoos.

Conservation Strategies

The best model for preserving and reintroducing tamarins is provided by that designed for the golden lion tamarin as formulated by researchers at the National Zoo (Mallinson, 1984). Golden lion tamarins are the most carefully managed exotic animal in captivity. Mallinson (1984) proposes that zoo curators cooperate in the sharing of information regarding the medical histories and pedigrees of their animals to minimize inbreeding, maximize heterozygosity, and prevent the genetic over-representation of individuals in the population (Wharton, 1984).

There is a critical need for the establishment of secure reserves in both Colombia and Panama. Research must be conducted to determine which remaining areas are critical for the successful maintenance of these tamarins, and such areas must be sequestered. There should be a total ban on the hunting, collection, and exportation of both the Colombian and Panamanian forms of tamarins. The remaining wild populations should be censused and managed, and, where possible, schemes involving reforestation of damaged habitats and transplantation of animals from those areas with reduced carrying capacity should be designed. Breeding colonies should be established in exporting countries as well as in those that traditionally have imported tamarins for biomedical research (Kleiman, 1978). Reintroduction schemes, which have already proven to be partially successful with golden lion tamarins, should be adapted for cotton-top tamarins (Konstant & Mittermeier, 1982). Animals that are targeted for reintroduction should be provided with the most ecologically relevant captive environments possible to facilitate their preparedness for a return to the wild.

Management of Callitrichids in Captivity

In order to improve the survival and reproductive rates of captive Callitrichids, the increased understanding of their natural histories must be applied to captive husbandry and management strategies. Some improvements in captive maintenance include: increasing the vertical complexity within the enclosure; exposing the animals to more natural photoperiods; maintaining temperature and humidity levels at those reminiscent of natural habitats; providing more varied diets; reducing handling for veterinary procedures; providing more secluded nest boxes for pregnant females; and providing a more adequate social environment. These changes appear to reduce stress, as measured by reductions in aggressive interactions. The reduction in aggression has enabled juveniles to remain with their parents during succeeding births as they do in the wild, thus improving their opportunity to develop social competence and adequate parenting skills (Heltne, 1978; Ogden, Wolfe, & Dienhardt, 1978). These habitat alterations have also improved the reproductive performance of cotton-top tamarins (Tardiff, Carson, & Clapp, 1986).

Improved reproductive success is correlated with increased enclosure size (Fontaine & Hench, 1982). Enlarging enclosures from the typical 0.20 m^3 to 3.0 m^3, results in a 50% increase in the survival rate of infants (Tardiff, Carson, & Clapp, 1986).

An increase in the vertical complexity within enclosures can facilitate the expression of species specific locomotor activities. Climbing structures and ledges should be features of every contemporary enclosure. Ledges and nest boxes should be incorporated into enclosures to enable animals to withdraw from aggressive encounters or to engage in social interactions with mates (Snowdon, Savage, & McConnell, 1985).

Although modern commercial diets are adequate, they should be supplemented with vitamin D_3, fresh fruits, vegetables, and protein, often in the form of live insects. Food-related competition can sometimes be reduced by modification of the feeding regimen by supplementing the regular diet with randomly distributed forage, and by separating animals spatially and temporally (Kirkwood & Underwood, 1984).

Temperatures within enclosures should be maintained near 24°C (75°F), and relative humidity should be maintained near 70% (Brand, 1981).

Photoperiod acts as an exogenous modulator of endogenous oscillators through the suprachiasmatic nucleus and exerts profound influences on cyclicity in seasonally reproductive species (Erkhart, Nagel, & Stephani, 1986). Artificially controlled photoperiods should be regulated in a manner that replicates the diurnal and seasonal photoperiodic patterns of natural habitats. When feasible, animals should be exposed to the full spectrum of electromagnetic frequencies characteristic of natural light (Walker, 1975). Traditionally, Callitrichids, along with most other laboratory primates, have been housed in large colonies. Communal housing has been associated with elevated levels of aggression, especially toward iso-sexual conspecifics (Dawson, 1979; Kleiman, 1978; Neyman, 1978). In nature, this aggression probably serves to drive animals approaching maturity from the family group, reducing the possibility of inbreeding and facilitating the formation of new family groups (Hoage, 1982; Neyman, 1978).

In light of this knowledge, aggression in colonies of Callitrichids can be reduced if animals are housed together in single, heterosexual pairs of socialized adults (Garber, Moya, & Malaga, 1984). Juveniles should be allowed to remain with their parents through at least one cycle of reproduction, but should be removed as they approach puberty. This separation not only reduces the risk of increased levels of agonism, but releases sub-dominant females from the reproductive suppression imposed on them by dominant females, potentially improving their reproductive potential.

The combination of effective conservation and management strategies should enhance the future prospects of Callitrichids, including cotton-top tamarins.

Problems with Captive Animal Research

Observing and interpreting the behavior of animals is fraught with problems. Many of the same difficulties encountered by the field researcher are encountered by researchers in the zoo. If anything can go wrong with a behavioral enrichment scheme, it will (Markowitz, 1982). Perhaps the greatest problem encountered in observing the behavior of captive animals is the singular lack of control that the researcher has over the conditions under which the study is conducted.

The behavioral researcher in the zoological garden must work within the zoo's established husbandry routines (Kleiman, 1985a). This can restrict the times during which data can be collected, sometimes an important consideration in studies involving nocturnal or crepuscular species (Erkert, Nagel, & Stephani, 1986). For example, the data set discussed here was collected during regular zoo visiting hours, i.e., between 10:00 hours and 17:00 hours. Tamarins, however, are crepuscular animals (Terborgh, 1983) and exhibit their highest levels of activity in the early morning, between 06:00 and 07:30 hours (Garber, 1984b), before observers are permitted to enter the zoo.

The problems encountered by zoo researchers collecting data when visitors are present, during regular visiting hours, are even more complex. Visitors often deliberately or unwittingly elicit responses from animals while researchers are attempting to collect data. Some of the interference is so pervasive that data are unusable. These behaviors include provocative gestures and vocalizations, offering of novel food and non-food items to the animals, and striking or breaching the enclosure. These inappropriate actions can directly influence the behavior of an animal as it attempts to evade a threatening aspect in its surroundings, or there can be an indirect influence on behavior resulting from elevated levels of stress. During the course of this study, the data from many sampling sessions had to be discarded because of zoo visitors pounding on the glass wall of the tamarin enclosure.

While sources of behavioral variability can include the actions of zoo visitors, animals are also affected by inappropriate quality and quantity of space (Hediger, 1950/1964), unnatural light cycles (Hobbs, 1981), and excessive sound pressure levels (Gamble, 1982) which can result in increased levels of reactivity possibly indicative of stress. Many experimental procedures involving the manipulation of some environmental parameters (e.g. sound levels) can themselves increase stress in captive animals. The sound pressure level of playback variables used in research must be carefully considered. Excessive sound pressure levels are potentially harmful to many animals (Gamble, 1982). Acoustic playback studies ideally should employ sound pressure levels similar to those encountered by an animal in its natural habitat (Dabelsteen, 1981). The amplitudes of acoustic phenomena that occur in nature, however, are seldom available and must be estimated, often incorrectly, possibly reducing their ecological validity.

The number of variables and order of their presentation can influence the probability of encountering habituation, anticipation, or perseveration. Habituation is especially troublesome in longitudinal studies featuring a limited number of treatment variables. While a limited number of variables facilitates data analysis, the danger of overexposing subjects to them is real. The problem is exacerbated by fixed interval presentations, which are often mandated by technical and financial constraints. For example, the use of mechanical timers precludes variable interval treatment presentations. Another technical limitation of the present study concerns the order of the playback variables, which were fixed on a master recording and could not be varied. All of these design limitations increase the probability of habituation.

The presence of unnatural sounds can also impact the effectiveness of this type of research. In addition to the unnatural sounds typically present in zoological parks, this research was occasionally confounded by the presence of portable radios brought into the food preparation areas behind the enclosures by keepers. It is conceivable that this noise operated as an acoustic masker and lowered the responsiveness of the subjects to the treatments.

While the use of multiple observers allows more data to be collected at different times, it also introduces the problem of inter-rater reliability (Rawls, *et al.*, 1982). This potential problem is partially addressed by training, inter-rater reliability tests, and the use of one-zero sampling, which yields a relatively high level of agreement between observers (Lehner, 1979).

No matter how well observers are trained, some behaviors are more easily observed than others. Subtle interactions such as tactile and olfactory behaviors are usually underestimated by observers, while vocalizations and visually mediated behaviors are usually overestimated (Dolan & Bramblitt, 1982). These shortcomings can be partially addressed by providing observers with clear operational definitions; the absence of which represents another broad class of potential problems in behavioral research.

Research that involves the recording and playback of acoustic phenomena is fraught with potential problems. Not only must any acoustic treatment variable be presented at an appropriate sound pressure level, but the signal should be as free from distortion as possible. Distortion in a playback variable might reduce its ecological relevance to the subjects and dampen their rates of response. Another question that must be addressed is that of the possible intrinsic ecological relevance of each acoustic variable. Often, experimental variables are chosen because of their availability or on the basis of claims made by other researchers. Even more troublesome than understanding the function of vocalizations is attempting to determine which of several animals is generating them. Complex telemetric monitoring systems are required to identify the vocalizing animal accurately (Mackay, 1970). Minimally, any system employed in monitoring the acoustic behavior of animals should be multi-channeled. A single-channel system, as was employed in this study, will not allow observers to determine which animal is responding. Consequently, while other behaviors can be reliably attributed to specific subjects, an additional category of unidentified was required to accommodate the many vocalizations that could not be clearly attributed to a specific animal.

There are various technical problems associated with recording and playback equipment. In many instances, its initial quality is limited by budgetary constraints. In the zoo environment, equipment is subject to rapid degradation through exposure to corrosive substances, including cleaning fluids and urine. Transducers in enclosures often become objects of interest to animals and are susceptible to physical damage. Microphones are especially difficult to shield from extraneous magnetic fields encountered in enclosures with fluorescent lighting. Fluorescent lights can impose a harsh-sounding 60 Hz signal over any program material being recorded and/or played back. For example, after the installation of the recording equipment in the newly constructed tamarin enclosure, fluorescent lighting was installed in the food preparation area, one meter above the microphone. This unfortunate situation resulted in the induction of a harsh 60 Hz buzz into all recorded program material. Various attempts to reduce this noise met with only marginal success. All components involved in the recording system were carefully grounded, shielded, or placed in Faraday cages (Mackay, 1970). Line filters were installed on all equipment operating on 117 v.a.c. line current.

Another broad area of concern is the adequacy of the sampling instrument. In designing an instrument for use by multiple observers with varying levels of proficiency, there must be some degree of reduction in the number of dependent measures. This broadening of categories often reduces the resolution of the sampling instrument, and by extension, the data. In many instances, the most interesting behavior observed during this study could not be classified into the scheme imposed on observers by the sampling instrument. More extensive reconnaissance research could reduce the problem of inadequate sampling instruments featuring irrelevant or incomplete numbers of categories.

Problems notwithstanding, the contemporary zoological garden offers a unique opportunity to study a diversity of exotic species at close range, in order to better understand the influence that captivity exerts on behavior. The following is an account of research that attempts to determine the degree to which environmentally relevant acoustic phenomena influence the frequencies of several typical behaviors in a pair of captive cotton-top tamarins.

MATERIALS AND METHODS

Subjects

The subjects used in this study were two adult cotton-top tamarins (*Saguinus oedipus oedipus*) housed together at the Primate Discovery Center of the San Francisco Zoo. The female was 23 months old while the male was 24 months old at the beginning of the study. The female was born on August 26, 1983, at the Lincoln Park Zoo in Chicago, Illinois. She was mother-reared and continued to be housed with her parents during succeeding births. She arrived at the San Francisco Zoo on June 6, 1984 and was held in quarantine in the zoo's hospital for several weeks after her arrival. After the quarantine period, she was transferred to the Children's Zoo, where she remained with the male until construction of the Primate Discovery Center was completed, a period of approximately one year.

The male was born on August 8, 1983, at the Buffalo Zoo in Buffalo, New York. Some confusion exists regarding his early history; at the time of his birth, his parents were on breeding loan from the Utica Zoo, from which he was purchased by the San Francisco Zoological Society. Although there is uncertainty about the length of time that he spent with his parents, it is thought that he was removed from his family group prior to the births of any siblings. He arrived at the San Francisco Zoo on August 9, 1984 and placed in quarantine for several weeks after which time he was introduced to the female, and then housed at the Children's Zoo, where he remained for approximately one year.

While they were housed at the Children's Zoo, contact with the animals was limited to the maintenance staff and volunteer caretakers. On April 22, 1985, the tamarins were transferred to their newly completed enclosure at the San Francisco Zoo's Primate Discovery Center. They were allowed to habituate to their surroundings for 2 months prior to the beginning of the study.

Reproductive History

On July 3, 1986, 2 newborn tamarins were discovered in the enclosure, 437 days from the time of the pair's introduction to the exhibit. This is well in excess of the normal 305 day gestation period reported for cotton-top tamarins by Evans (1983a). The following day, both infants were found dead on the bottom of the enclosure, each bearing multiple bite wounds. This discovery is in keeping with the findings of Kilborn, Sehgal, Johnson, Beland, and Bronson (1983), which suggests that primiparous females and animals with no peer rearing experience possess poor parenting skills. Another pair of infants was born in January, 1987, yielding an interbirth interval of six months, considerably shorter than those reported by Evans (1983a). The male of this pair was stillborn, but the female was born alive. The mutilation of the first pair of infants prompted the zoo management to remove the female from her parents, though she was later returned to them. At birth, the female weighed 45.7 g while the male weighed slightly less, possibly an artifact of a missing hand.

Glatson, Geilvoet-Soeteman, Hora-Pecek, and van Hooff (1984) report that the zoo environment can strongly influence the behavior of female tamarins toward their young, and suggest that they should be placed off exhibit during parturition to minimize inappropriate responses to their infants.

Diet and Maintenance

Although some food was always available to the animals, the main feeding occurred daily between 09:30 and 10:30 hours. On a regular basis, the animals were provided with: bananas, grapes, apples, celery, green beans, raw and cooked sweet potatoes, raw and cooked carrots, dead crickets, and live meal worms. Occasionally, live crickets (*Acheta domestica*) were placed in the enclosure to provide foraging opportunities for the animals. Felovit and Abdick vitamin supplements were regularly added to the diet to increase levels of vitamins B_3 and D_3. This feeding regimen follows closely the suggestions of Kirkwood (1983) and Brand (1981).

Cotton-top tamarins are susceptible to colonic disorders, which are strongly influenced by their diets (Eskajadillo, Bronson, Sehgal, & Hayes, 1981). They are also susceptible to respiratory disorders, for which they were constantly monitored, and which were detected several times during the course of the study. When antibiotics were required, they were administered in powder form after being applied to grapes or bananas.

The animals were also continuously monitored for any external signs of injury or disease. Fecal samples were routinely examined for the presence of parasites. Tamarins are especially susceptible to infestation by nematodes of the genus *Strongyloides*. Infestations of this type were treated by administering Nabandisol or Talmin.

On October 29, 1986, the female was treated for an abscess on her left cheek. This abscess resulted in a permanent scar which assisted the observers in distinguishing her from the male.

Habitat

The tamarins were housed in a rectangular terrarium-style enclosure with external dimensions of 13 ft. X 7 ft. 3 in. X 9 ft. 6 in. The southeast corner, where data collection activities were concentrated, was curved, with a radius of 1 ft. On the south and east sides of the enclosure, a concrete base 18 in. high supported an 8 ft. high glass wall, 6 ft. of which were visible to the public. The north and west walls were constructed of concrete. Keeper entry was provided by a door in the lower west wall of the enclosure.

The floor of the interior sloped toward the rounded southeast corner, where a filtered drain protruded 6 in. above the concrete base. Filtering was accomplished by surrounding the drain aperture with 2 to 3 in. of gravel and several layers of fiberglass. This entire assembly was housed in a perforated PVC pipe that served as a coarse filter, while not obstructing keeper access to the drain. The entire bottom of the enclosure was covered to a minimum depth of 1 ft. with equal parts of UC Mix and sphagnum moss. Sonoma fieldstones imbedded in the substrate provided a path for use by the keepers.

Several large angle brackets were permanently installed in the base, providing mounting surfaces for large branches, intended to serve as the primary climbing structures within the enclosure. These brackets were slotted so that the angle of the branches could be periodically changed. Greater vertical complexity was added to the habitat by attaching additional limbs to the primary branches.

On the two concrete walls, chicken wire mounted in a redwood frame originally supported a layer of sphagnum moss and bromeliads (*Telancia spp.*). This arrangement proved too difficult to maintain and was removed before the completion of the study. Other plants in the enclosure included *Fiscus rubra, F. elastica*, and *Telancia xerographica*. *F. rubra* was chosen to contrast its large leaf size to that of the diminutive tamarins.

At any time, one or two nest boxes were available to the animals. These were positioned on the west wall, at least 48 in. above the substrate.

The enclosure was watered manually through hosing, which hydrated the plants, cleansed the enclosure, and elevated the relative humidity, which ranged from 65 to 70%. The temperature ranged from 65°F to 75°F, with a mean of 70°F. This is somewhat lower than the 78°F to 80°F recommended by Brand (1981). Originally, temperature and humidity were to be regulated by a centralized climate control system. This mechanism was never fully operational during the course of this study. Therefore, additional heat was provided by several 150 W and 500 W heat lamps, which were suspended from the top of the enclosure along its south wall. Several lower wattage lamps were operated continuously to increase illumination, while the higher wattage lamps were operated cyclically when additional heat was required.

Materials

Sound Equipment

The sound equipment used in this study included the following:

Dayton 2E-408 repeat cycle timer

General Radio 1565B sound pressure level meter ("A" weighted)

Heath IG-1271 signal generator

Industrial EK-1455 precision timer

JVC KD-V200 stereo cassette recorder

JVC CS-610 6 in dynamic loudspeakers (40 Hz to 18 kHz)

Kay 7800 Digital Sonograph

Nikko TRM-40 integrated stereo amplifier

Realistic MPA-35A power amplifier (35 W rms)

Revox A-77 1104 stereophonic reel-to-reel tape recorder

Sharp CT-660E digital timer

Sony F-96 dynamic cardioid microphone

Sony FU-30T cardioid dynamic microphone (80 Hz to 14 kHz)

Sony MDR-1 headphones

Sony 105-A monophonic reel-to-reel tape recorders

Sampling Instrument

The relevant literature was reviewed and abstracted to formulate an ethogram for cotton-top tamarins. Based on earlier research, e.g., Cleveland and Snowdon (1982) and Moynihan (1970), hypotheses were formulated. A subset of the behavioral repertoire of cotton-top tamarins was selected to serve as dependent measures throughout the course of the study (Lehner, 1979).

The sampling instrument employed in this study closely follows design suggestions presented in Lehner (1979) and Martin and Bateson (1986). Both events and states are recorded in the form of modified frequencies from which information regarding relative numbers of occurrences and durations of behaviors are extrapolated. The sampling method could be referred to as an obligate focal dyad technique, determined by subject availability (Altmann, 1974).

The sampling instrument on which data were recorded consisted of an 8-row X 10-column data matrix (see Appendix A). Each row represented a specific dependent variable and was divided into thirds representing male, female, and unidentified animal. Dependent variables included: allogrooming; autogrooming; visual scanning; scent marking; sexual behavior; display; foraging/ environmental exploration; vocalizations; and not visible. Each of the 10 columns represented 30 second data collection periods. These columns were further divided into two groups of five columns each, providing for 2 2.5-minute data collection periods for each data sheet. As well, each data sheet contained 10 8-cell grids for noting the location of each animal within the enclosure.

The enclosure was conceptually divided into eight equal segments, four upper and four lower quadrants, in a manner similar to that employed by Caine (1984) and Yanofsky & Markowitz (1978). The upper and lower sections of the enclosure were defined by a seam on the maintenance access door. Each segment was designated by a three letter code derived from the location of the quadrant within the enclosure:

RUB--right upper back, northeast corner;

LUB--left upper back, northwest corner;

RDB--right lower back, northeast corner;

LDB--left lower back, northwest corner;

RUF--right upper front, southeast corner;

LUF--left upper front, southwest corner;

RDF--right lower front, southeast corner;

LDF--left lower front, southwest corner.

Additional space was provided on each data sheet for including the time, date, name of observer, occurrence of feeding, urination, defecation, and other behaviors for which specific categories had not been provided.

Ambient Sound

Ambient sound levels were measured with a General Radio Company 1565B sound pressure level meter. The meter was held at a height of approximately 3.5 ft. from the ground and 2 ft. away from the user to minimize the alteration of sound pressure levels by the experimenter.

Ambient sound pressure levels, recorded near the Primate Discovery Center on a typical weekday, ranged from 65 dB to 70 dB. Near the maintenance room where the primary recording system was housed, the mean ambient sound pressure level ranged between 57 dB and 66 dB, depending on the number of visitors within the zoo. Within the equipment room, the sound pressure level ranged from 77 dB to 85 dB, reaching the higher level when air conditioning compressors were operating. Near the southeast corner of the tamarin enclosure, where the data collectors were located, the ambient sound pressure level averaged 55 dB.

Within the tamarin enclosure the ambient sound level ranged from 50 dB to 53 dB. When the treatment variables were administered, the interior sound pressure level ranged from 67 dB to 71 dB.

The enclosure provided some degree of isolation from the acoustic environment of the zoo. This level of attenuation was determined by using a Heath IG-1271 audio frequency signal generator to produce sinusoidal sounds at test frequencies of 1.0 kHz and 10 kHz. Both test frequencies were produced within the enclosure at a known SPL and the SPL was measured outside of the enclosure. The level of attenuation provided by the glass wall of the enclosure averaged at least 20 dB (10%) at both test frequencies.

Location of Experimental Equipment

Two separate sound systems were installed in the enclosure prior to the completion of the Primate Discovery Center. One system facilitated the monitoring and recording of all acoustic phenomena occurring within the enclosure, while the other allowed acoustic treatments to be presented to the subjects.

On the west wall of the enclosure an aperture housed a Sony FU-30T cardioid dynamic microphone connected by a balanced line to a Realistic MPA-35 amplifier and a Sony TC-105 reel-to-reel tape recorder. The microphone allowed for the simultaneous recording of acoustic phenomena within the enclosure and presentation of the sounds to the public.

Two JVC-C610 speakers which received the output from a Nikko TRM-40 integrated stereo amplifier were mounted within apertures near the top of the enclosure along its west wall. A JVC KDV-200 stereo cassette recorder, controlled by an Industrial EK-1455 scientific timer, was connected to the amplifier input. A Dayton 2E-408 repeat-cycle timer controlled the scientific timer, which it triggered every 20 minutes, activating the cassette recorder for 45 seconds. This dual timer system provided a mechanism for controlling the repeated timed playback of sounds to the animals and public.

A sixty minute cassette was programmed with four repetitions of a sequence of eight different acoustic treatments. Each treatment was fifteen seconds in duration and separated from adjacent treatments by 45 seconds of blank tape. Detailed descriptions of the treatment variables are presented in Appendix B.

Recordings of acoustic phenomena within the enclosure were made on Sony TC-105 and Revox A-77 reel-to-reel tape recorders operating at 7.5 IPS. At this speed, the frequency response of the Sony ranged from below 40 Hz to well above 18 kHz, while that of the Revox A-77 ranged from below 30 Hz to above 22 kHz. Another Sony TC-105 tape recorder, located outside the enclosure and near the observers recorded real-time verbal accounts of the data collection.

Procedure

From June 9, 1985 until July 1, 1985, a reconnaissance study was conducted to test the validity of the dependent measures and to optimize the format of the sampling instrument, a procedure suggested by Lehner (1979).

A baseline study was conducted from August 8, 1985 to October 31, 1985, during which no treatment variables were presented to the animals. This was followed by an experimental protocol that extended from December 5, 1985 to June 20, 1986, utilizing eight acoustic treatment variables to test the hypothesis that auditory stimulation could influence the behavior of captive cotton-top tamarins.

Experimental Protocol

Six observers were inducted from the docent core of the San Francisco Zoological Society and from the Biology Department of California State University at San Francisco. All participants were trained in observing the subjects before the beginning of data collection. Prior to the inception of the study proper, inter-rater reliability tests were conducted to ensure that the six observers exhibited a high degree of agreement in their interpretation and recording of behavior (Ralls, Lundrigan, & Kranz, 1982). After the completion of the study a second inter-rater reliability test was conducted to determine if the level of agreement had been maintained throughout the course of the study. Inter-observer agreement never fell below 89%, and typically exceeded 91%. This high correlation allowed observer identity to be removed as an independent variable when the data were analyzed. Data collection was begun on August 8, 1985 and completed on June 20, 1986. The baseline data were collected between August 8, 1985 and October 31, 1985. Beginning on December 5, 1985, presentation of the treatment variables was begun and continued until June 20, 1986.

Data were collected exclusively during weekdays, to control for any influences that the increased number of visitors present in the zoo on weekends might exert on the behavior of the subjects. Data collection was conducted between the hours of 9:00 A.M. and 4:00 P.M.--with the majority of collections occurring between 1:00 P.M. and 4:00 P.M.--for a maximum of 3 hours per day. This limitation on the number of daily playbacks was chosen to minimize habituation effects, a severe problem with playback studies (Cleveland & Snowdon, 1982).

At the beginning of each day during which data were collected, observers were situated at the southeast corner of the enclosure and the primary timer was activated. Every 20 minutes, one of eight acoustic treatment variables was presented to the subjects. The fixed interval treatment presentation was a design limitation imposed on this study by the use of mechanical timers, though it is similar to procedures employed by Cleveland and Snowdon (1982).

Data were collected for a period of 2.5 minutes, every 10 minutes. This procedure meant that the behavior of the animals was measured during and immediately following stimulus presentation and then again during an intertreatment interval between stimulus presentations.

Each 2.5 minute session was subdivided into 5 30-second intervals. During each 30-second interval, observers scanned the data sheet and recorded the occurrence or nonoccurrence of each behavior and the location of each animal. Simultaneously, all vocalizations were monitored through headphones. At the conclusion of each 2.5 minute collection period, the data were summed and the behavior of the subjects was discussed by the observers. Observers were encouraged to record any novel or potentially important behaviors other than those listed on the sampling instrument in its comment section, a procedure recommended by Ralls, Lundrigan, and Kranz (1982).

Data from each sheet were summed, entered into a computer, and tabulated with Statistical Package for the Social Sciences PC+, Version 4.0.

Experimental Design

The overall configuration of this study is a within subjects, repeated measures design. This quasi-experimental study consists of a baseline and a treatment level. This format is often employed in research involving limited numbers of subjects.

Sampling Method

Data were collected using a one-zero sampling method (Hansen frequencies; Box & Morris, 1980). This technique records the presence or absence of a specified activity during a prescribed time interval. The actual numbers of occurrences are not recorded, rather the number of intervals during which an activity occurs at least once is recorded.

The one-zero sampling method has the advantage of providing high inter-rater reliability when a study employs several observers (Ralls, Lundrigan, & Kranz, 1982). Although this sampling method tends to underestimate the frequencies of short duration events and overestimates the frequencies of longer duration events (Kraemer, 1979), it provides a reliable index of their relative rates of occurrence (Rhine & Linville, 1980). One-zero sampling has been criticized for lacking validity (Altmann, 1974), though comparisons of

Hansen frequencies with other sampling and recording methods, including all occurrences, reveals that these scores correlate at levels approaching 0.90 with other types of scores. One-zero scores offer a means of estimating both rates and durations of behavior, in addition to providing a valid single measure of social relationship (Rhine & Flanigan, 1978). Data recorded in this form possess the advantage of already being partially reduced even as they are recorded, decreasing the incidence of error during data reduction (Baulu & Redmond, 1978).

Data Presentation and Analysis

The data represent total one-zero scores for each animal under 17 different conditions (see Appendix C). An appropriate statistic for small sample size studies is the chi-square (Siegal & Castelan, 1956). The expected frequencies for the analysis were derived from the baseline scores (condition 0). These totals were then compared to the totals for each behavior by each animal under 16 different conditions. An investigatory omnibus chi-square test was conducted to detect any significant treatment effects, followed by 216 individual planned comparisons in order to detect significant individual effects.

Dependent Variables

Operational definitions of dependent measures include:

Allogroom: One animal grooms another with hands, digits, lips, or teeth. Individual bouts are circumscribed by intervals of at least five seconds during which no allogrooming occurs.

Autogroom: An animal grooms itself with its own hands, digits, lips, or teeth.

Grooming is defined as any of several tactile behaviors that involve manipulation of the pelage of an animal by itself or by another using the digits, lips or teeth (mandibular tooth comb). Grooming can involve the use of the hands to part the fur while the digits are used to remove particulate matter from the pelage of itself or another animal (Sparks, 1969). Grooming can be solicited by an animal adopting a sprawling, supine posture while in view of another animal (Moynihan, 1970).

Intimately associated with grooming is approach, a cautious closing of the distance between two animals. Another behavior associated with grooming is huddling, the adjacent positioning of two animals with large areas of their bodies in contact with one another.

Scanning: This is a low level vigilance behavior performed at regular intervals by tamarins at high baseline levels to assess the immediate surroundings. Scanning involves a rapid sweeping motion or a lateral flick of the head in the horizontal plane for periods of up to ten seconds, providing a field of view approaching 360 degrees. It can be performed from a standing or sitting position.

Scanning functions as an anti-predator behavior and occurs in response to novelty in the environment, persisting even in relatively benign captive habitats. This action is used in intracage and extracage surveillance and is directed at both inanimate and animate objects (Caine, 1984, 1986; Terborgh, 1983). This behavior is distinct from visual inspection, which often follows detection of a novel object and does not involve the continuous lateral motion of the head (Caine, 1984; 1986); head tilting, which is involved in increasing retinal disparity to improve binocularity (Snowdon, personal communication, November, 1986); and head flicking, also important in increasing binocularity and characterized by two or three almost imperceptible lateral vibrations of the head.

Scent Marking: Scent marking includes a group of locomotor behaviors that facilitate the deposition of metabolic products onto substrates in the environment (Epple, 1975; Sutcliffe & Poole, 1978).

Anogenital scent marking involves marking with the super pubic glandular field or with the circumgenital glandular field. It can also involve sit rubbing, which may also deposit urine and feces in addition to glandular secretions. Animals engaging in these behaviors perform front to back or lateral movements of the pelvic girdle, with some portion of the perineal integument in contact with the target surface.

Sternal scent marking involves pressing the sternum against the substrate and pulling the body forward in a slow forward progression with the front limbs. Muzzle rubbing is implicated in the deposition of mucous and saliva onto substrates. This behavior involves the prolonged placement of the muzzle adjacent to a target object and is often accompanied by frontal-lateral motions of the head, often with a slow forward progression along the target substrate toward a target object.

Sexual Behavior: This category of behaviors includes mounting with and without thrusting and intromission.

Mounting is characterized by the typical mammalian mating stance wherein the ventrum of the male is positioned over the dorsal posterior surface of the female. Thrusting and intromission may or may not be a component of an episode of mounting. When copulation occurs, the male clasps the female around the waist, initially with the hind feet planted on the substrate. Sometimes the male will press his face into the pelage on the nape of the neck of the female while tightly closing his eyes and wrinkling his nose. During some particularly vigorous copulations, the male may appear to attempt to climb up the back of the female.

Although they are difficult to observe, from three to twenty intromissions can occur before the male dismounts. Thrusting can occur without intervaginal intromission and intromission can occur without ejaculation. Ejaculation is characterized by a change in the tempo of pelvic thrusting and a prolonged terminal intromission. Often, there is a cessation in sexual activity immediately following a successful copulation (Moynihan, 1970).

Genital Display: This class of behaviors includes several distinct types of genital displays, including those wherein the animal presents its posterior, with the tail elevated to expose the scrotum, primarily to iso-sexual animals and human observers (Wendt, 1979).

Penile Display: This is a genital display characterized by the approach of the animal toward the target and the opening of its legs, exposing the erect penis as it faces the recipient.

Bipedal Stance: This is a posture that emphasizes the strong countershading of the ventrum. This display often involves a slow, sinuous lateral swaying.

All three displays are observed in aggressive or agonistic interactions. Each may involve some degree of piloerection, indicative of elevated levels of arousal. Piloerection also occurs when animals are startled by sudden or novel phenomena in their surroundings. Piloerection can involve the entire pelage or only specific portions, e.g., the cephalic plumage. The amount of piloerection is correlated with the intensity of the arousing stimulus (Moynihan, 1970). Low levels of arousal result in piloerection of only the tip of the tail. As the strength of the stimulus increases, more of the hair along the dorsal ridge, up to and including the cephalic plumage, becomes involved.

Foraging/Environmental Exploration: This is defined as browsing within and manipulation of some aspect of the environment.

Foraging and environmental exploration constitute a general class of exploratory and manipulative behaviors that can be food related. Food related foraging is more directed and object oriented than investigatory foraging. Foraging is distinguished from feeding by its investigatory and acquisitive function, while feeding features consumptive behavior. Foraging not related to food often involves low levels of nondirected investigatory behaviors. Target objects are often subjected to close visual, olfactory, or tactile investigations, and include components of the substrate, vegetation, or novel objects within the enclosure. Objects are often manipulated with the digits or mouth. These same behaviors often precede the ingestion of food. Foraging animals often display a slow, forward quadrupedal progression along the substrate or ascend into vertical or oblique branches, usually at low basal levels.

Vocalization: These are any of several species-specific acoustic emanations from the mouth of the subjects.

Some of these sounds are produced with open mouths and are clearly audible, while others are produced with closed mouths at low amplitudes and are difficult to score. The vocal repertoire of Callitrichids in general, and cotton-top tamarins in particular, is treated more extensively elsewhere in this report.

Not Visible: This is a state that is scored positively when either subject can not be located by observers. It does not imply that other behaviors have ceased to occur, especially vocalizations.

This category is included to fulfill the requirement that the list of dependent measures be exhaustive.

A more extensive Callitrichid ethogram can be obtained from Coates and Poole (1983), Cleveland and Snowdon (1982), or Moynihan (1970), from whose work the above categories and definitions were abstracted.

Independent Variables

Playback variables consisted of eight different sounds, seven of which were derived from two related subspecies of tamarins and one from a common insect prey item. Tamarin vocalizations were obtained from two sources. Vocalizations of *Saguinus oedipus oedipus* were recorded in 1982 at the Wisconsin Regional Primate Center at the University of Wisconsin. These recordings were obtained by courtesy of Dr. Charles T. Snowdon. These calls could have been produced by any of a number of tamarins that were housed in a large breeding colony and separated into discrete family groups. The tapes were processed at the University of Wisconsin with a 600 Hz high-pass filter for all calls except those containing "F" chirps. These calls were filtered at 3.0 kHz, below the fundamental frequencies of "F" chirps, with no appreciable loss of information (Snowdon, personal communication, 1985). In both cases, the filtering was undertaken to reduce cage noise. Playback variables featuring vocalizations of *Saguinus oedipus geoffroyi* were obtained from a free living troop of tamarins consisting of three adults and several juveniles, recorded in Poco, Panama over several mornings in July, 1982. These recordings were obtained by courtesy of Ken Gold. The manufacturers and models of the original recording equipment could not be obtained from those providing the source recordings.

In order to maximize the ecological relevance of the playback variables, their amplitudes were adjusted in accordance with the work of Green (1975), Dabelsteen (1981), and Seyfarth, Cheney, and Marler (1980), each of whom employed acoustic treatments with sound pressure levels ranging from 57 dB to 62 dB. Recordings of vocalizations from the subjects were made and were found to feature amplitudes ranging from 57 dB to 71 dB. When the ambient noise level in the enclosure was considered and combined with that of the acoustic treatments, the actual sound pressure levels during treatment presentations ranged from 67 dB to 71 dB. Consequently, the treatment variables were administered to the subjects within this range of intensities. There was a general desire to employ the lowest possible effective sound pressure level. Excessive amplitude can result in rapid habituation, cessation of response, or actual injury to the test subjects (Gamble, 1982). Conversely, insufficient amplitude can result in reduced rates of response (Dabelsteen, 1981).

Predictions about the probable responses of the subjects to the vocalizations of *S. o. oedipus* are based on the work of Cleveland and Snowdon (1982). Predictions about the probable responses of the subjects to the vocalizations of *S. o. geoffroyi* are more problematic, and are based on the work of Moynihan (1970; 1976).

The description of each playback variable with predictions are as follows:

P.V. 1. The first playback variable in the sequence is an "F" chirp and a partial "F" chirp trill of captive *S. o. oedipus* (Cleveland & Snowdon, 1982). The "F" chirps are class one vocalizations. They are heard during intergroup vigilance activities and often occur in conjunction with normal long calls. "F" chirp trills are class two vocalizations and serve the same functions as "F" chirps but represent a slightly higher level of arousal. Animals hearing these vocalizations should respond with elevated levels of vocalizations, including combination long calls, "F" chirps, "F" chirp trills, and "F" chirp + whistle calls. The rate of scanning should also increase, while the rates of other measures should not be significantly affected.

P.V. 2. The second playback variable in the sequence includes recordings of vocalizations, especially trills of wild *S. o. geoffroyi* (Moynihan, 1970). These vocalizations are subjectively similar to "A" chirps, "G" chirps, "B" trills, and small, initially modulated whistles of *S. o. oedipus* (Cleveland & Snowdon, 1982). Tamarin vocalizations heard in the background are subjectively similar to vocalizations of *S. o. oedipus*, e.g., terminally modulated whistles, rapid whistles, large modulation multilevel calls, and other combination vocalizations. The vocalizations include "A" chirps, which are mobbing calls often given in response to sudden, animated stimuli. Components of "D" chirps are also present, which are often heard shortly after feeding. The behavior of the animals during the recording of these vocalizations included foraging and scent marking (Ken Gold, personal communication, 1985). The presence of "A" chirps, "G" chirps, "B" trills, and several types of whistles implies that the response of the subjects should be variable. Minimally, there should be increases in vocalizations and scanning. It is also conceivable that rates of scent marking and autogrooming might increase, especially if the subjects perceive these sounds as indicating the proximity of strange animals. The other measures should not be significantly affected.

P.V. 3. The third playback variable in the sequence is a recording of a cicada chorus, and was recorded on the morning of July 22, 1982 in Poco, Panama. There are 3 pulses comprising this chorus. The genus and species of the cicadas are unfortunately not known, but the insects are found near the wild troop of animals whose vocalizations were recorded for use in other treatment variables. This variable was included to determine if the presentation of a diffuse sound stimulus, especially that of a potential prey item, might result in an increase in environmental exploration and scanning. The other measures should not be significantly affected.

P.V. 4. The fourth playback variable in the sequence features vocalizations, especially trills and twitters recorded from a group of wild *S. o. geoffroyi* in Poco, Panama (Moynihan, 1970). Components of this sequence of calls are similar to the "B" trills, twitters, and background squeaks of *S. o. oedipus* (Cleveland & Snowdon, 1982). Background vocalizations contain elements that resemble "C" chirps, squeals merging into twitters, descending multiwhistles, partial quiet long calls, large modulation multilevel calls, and other combination vocalizations, again of *S. o. oedipus.* The twitters and trills are examples of class two vocalizations. The "B" trill is heard during the approach of an infant toward an adult, while the twitter appears to function in calming the infant. Squeals are heard when an active animal interacts with an unwilling passive animal, often in conjunction with wrestling or face pressing. The animals producing these calls were engaged in foraging activities and in investigating the observers (Ken Gold, personal communication, 1985). The subjects should respond with increases in the rates of scanning and vocalizing. It is also conceivable that the rates of autogrooming and scent marking might increase slightly, especially if the subjects perceived the sounds as indicating that a troop of unfamiliar animals is nearby.

P.V. 5. The fifth playback variable in the sequence is a recording of vocalizations that include "F" chirps, "F" chirp + whistle, partial quiet long calls, normal long calls, combination long calls, and small initially modulated single whistles from a group of *S. o. oedipus* located in a captive breeding group at the Wisconsin Regional Primate Center (Cleveland & Snowdon, 1982). Tamarins produce these vocalizations upon hearing distant sounding long calls from nongroup members. In response to this treatment, the subjects should display increases in the rates of scent marking, scanning, and vocalizing, especially with variants of the long call (Snowdon, Cleveland, & French, 1983). Typically, animals respond to these calls with increases in antiphonal calling, scanning, scent marking, and orientation toward the source.

P.V. 6. The sixth playback variable in the sequence is a recording of vocalizations that include trills and twitters produced by a pet *S. o. geoffroyi* in Panama (Moynihan, 1970). These calls are subjectively similar to class two "B" trills and twitters of *S. o. oedipus* (Cleveland & Snowdon, 1982). Some of these elements resemble vocalizations heard in conjunction with adult interactions with infants. The twitter component of the call should elicit increases in the rates of scanning and vocalizing in the subjects, while they emit the same vocalization in response.

P.V. 7. The seventh playback variable in the sequence includes vocalizations from captive *S. o. oedipus*, which exhibit components of both "C" chirps, descending multiwhistles, squeals, partial quiet long calls, and long call choruses, representing three classes of vocalizations (Cleveland & Snowdon, 1982). The "C" chirp is often heard just prior to the introduction of food in captive settings. Quiet long calls can be heard as animals cautiously approach unfamiliar stimuli. Both normal and quiet long calls are involved in intragroup and intergroup spacing. The quiet long call is more often observed as animals move quietly through their surroundings. This is an intratroop contact call and should elicit the same call in return (Snowdon, Cleveland, & French, 1983). These calls are also produced by animals that are quietly huddling, stationary, or engaged in low intensity foraging. The subjects should emit the same calls in response, or both animals should respond with a chorus of long calls. Expected responses to these calls also include increases in the rates of scent marking, scanning, and orientation toward the source. Other measures should not be significantly affected.

P.V. 8. The final playback variable in the sequence includes vocalizations, especially chirps and twitters produced by wild *S. o. geoffroyi* in Poco, Panama (Moynihan, 1970). These calls exhibit elements that subjectively resemble examples of several classes of vocalizations, including "A" chirps "G" chirps, multilevel whistles, twitters, "A" chirp chatter, "C" trills, and combination multilevel whistles of *S. o. oedipus* (Cleveland & Snowdon, 1982). These vocalizations were produced by a lone animal with an infant on its back. These calls should elicit an increase in scanning and vocalizing in the subjects. Their influence on the rates of other measures should not be significant.

A 2.56-second segment of each of the 8 15-second playback variables is reproduced in the form of a digital sonogram (see Appendix B). Sonograms were produced with a Kay Elemetrics model 7800 Sound Analyzer. The bandwidth was set at 0 Hz to 8 kHz with frequency markers set at 500 Hz, and analysis filter bandwidths set at 45 Hz.

RESULTS AND DISCUSSION

Results are based on comparisons between the baseline scores (condition 0) with those of each of the treatment conditions (conditions 1 through 8) and its respective intertreatment interval (conditions 1' through 8'); comparisons between the scores for each condition and its respective intertreatment interval; comparisons between the baseline scores (condition 0) with the combined scores for conditions 1 through 8; comparisons between the baseline scores (condition 0) with the combined scores for conditions 1' through 8'; and comparisons between the baseline scores (condition 0) with the combined scores for conditions 1 through 8'. Totals represent the combined scores for the male, female, and unidentifiable animals. 216 planned chi-square tests were performed; only results significant at P<.05 are presented. Totals are presented in appendix C.

Vocalizations

When the baseline scores are compared to the total treatment and intertreatment scores for identifiable animals, vocalizations significantly decreased with treatments ($\chi^2 = 4.26$, $n = 184$, $df = 1$, $p < .05$). When the scores for unidentifiable animals are included in the analysis (see Appendix E), vocalizations significantly increased with treatments ($\chi^2 = 136.1$, $n = 1429$, $df = 1$, $p < .001$) over the baseline vocalizations.

When the summed scores for playback conditions 1 through 8 are compared with the summed scores for intertreatment intervals (conditions 1' through 8'), vocalizations significantly increased, ($\chi^2 = 5.18$, n = 1022, $df = 1$, p = <.05).

The hypothesis tested with this measure states that vocal activity should increase in response to treatments featuring tamarin vocalizations that function in territorial encounters and intragroup spacing, i.e., all treatments except the cicada chorus (condition 3) (Cleveland & Snowdon, 1982; Epple, 1968; Moynihan, 1970).

The significant decrease in vocalizations recorded with some treatments was probably a result of the inability of observers to accurately ascribe the vocal response to a particular animal. The results obtained when the data for unidentifiable animals were considered were significantly different, with vocalizations being recorded more frequently during intervals featuring treatments than during those featuring no treatments. In virtually all cases, the subjects were more likely to vocalize during intervals featuring treatments than during intertreatment intervals. This finding suggests that the manipulation exerted an immediate and positive effect on the rate of vocalization.

There was a pronounced difference in the number of intervals during which vocalizations were attributed to the male compared to the number of intervals during which vocalizations were attributed to the female, with the male vocalizing approximately twice as frequently as the female. For example, during the baseline, the observers recorded vocalizations in 67 intervals for the male and in 39 for the female. These values were confounded by the recording of vocalizations in 389 intervals for animals that could not be positively identified. This sex related difference in responsiveness was consistent across all 8 treatments. In response to recordings of *S. o. oedipus*, the male vocalized in 7 intervals under condition 1, while the female failed to respond. Under condition 5, both subjects vocalized during 4 intervals. Under condition 7, the male vocalized during 1 interval, while the female failed to respond.

Under intertreatment conditions following recordings of *S. o. oedipus*, e.g., conditions 1', 5', and 7', the same sex related difference persisted. Under condition 1', the male vocalized during 9 intervals, while the female vocalized during 3. Under condition 5', the male vocalized during 3 intervals, while the female vocalized during 2. Under condition 7', the male vocalized during 3 intervals, while the female failed to respond.

Under treatments featuring recordings of *S. o. geoffroyi* the same sex related difference persisted. Under condition 2, the male vocalized during 4 intervals, while the female vocalized only once. Under condition 4, the male vocalized during 6 intervals, while the female vocalized during only 3. Under condition 6, the male vocalized during 3 intervals, while the female failed to respond. Under condition 8, the male vocalized during 3 intervals, while the female vocalized only once.

During intertreatment intervals immediately following the administration of sounds, the male consistently vocalized more than the female. Under condition 2', the male vocalized during 4 intervals, while the female failed to respond. Under condition 4', the male vocalized in 2 intervals, while the female failed to respond. Under condition 6', the male vocalized during two intervals, while the female vocalized only once. Under condition 8', both animals vocalized once.

Under condition 3, a recording of a cicada chorus, the male vocalized during 6 intervals, while the female failed to respond. Under condition 3', the following intertreatment interval, the male vocalized during 5 intervals, while the female vocalized only once.

When the baseline totals are compared to those for the treatment and intertreatment conditions, there is a significant increase in vocal activity. During the baseline, the total number of intervals during which vocalizations occurred, including those of unidentified animals, was 495, while during the treatment conditions it was 568, and for intertreatment intervals 454. The combined total of intervals during which vocalizations occurred was 1022, significantly higher than the baseline total of 495 ($\chi^2 = 136.00$, $P<.001$). When the totals for treatment conditions are compared to those for intertreatment conditions, and in the absence of data for unidentifiable animals, there was a significant increase in vocal activity under conditions featuring treatments compared to intertreatment intervals ($\chi^2 = 5.18$, $P<.05$).

These results suggest that there is a pronounced effect on the rate of vocal activity when animals are presented with certain acoustic phenomena and that the vocalizations of conspecifics can be employed to increase the rate of vocal activity in captive tamarins. Minimally, tamarins should emit alarm vocalizations in response to the perception of a strange animal (Epple, 1968; Moynihan, 1970).

The most commonly recorded vocalizations throughout this study included "F" chirps, "C" chirps, and variants of quiet long calls, two of which are associated with intertroop spacing, suggesting that the subjects were perceiving the playback treatments as representing the presence of strange conspecifics.

Some of these findings differ from those of Box and Morris (1980), who, in a study of mustache tamarins (*Saguinus mystax),* recorded significantly greater frequencies of vocalizations by females than males. Other researchers have found similar sex related differences in the rates of vocalization in other Callitrichids. However, Green (1981) has stated that, unlike polygamous, Old World cercopithecines, monogamous New World primates should exhibit fewer sex based differences in their responsiveness to the calls of conspecifics. Nonetheless, Cleveland and Snowdon (1982) and French and Snowdon (1981) reported that female cotton-top tamarins emitted long calls more frequently than males in response to the physical presence of, or sounds of, strange conspecifics. Female tamarins were more likely than males to give this call spontaneously, or in response to playback stimuli. Snowdon and Hodun (1985), however, reported that the reproductive state of the female exerted some influence on her rate of vocal activity. Nonreproductive females were significantly less likely to respond to the long calls of conspecifics than either receptive females or adult males (French & Snowdon, 1981). Moody and Menzel (1976) studied the vocal behavior of the saddleback tamarin (*Saguinus fuscicolis*) and found that the male vocalized more than the female. During the course of this study, under every condition, the male vocalized more than the female, often twice as frequently. However, Moody and Menzel (1976) also reported that there were considerable individual differences between subjects in responsiveness to acoustic stimuli. This finding should suggest additional caution in any interpretation of the present set of findings. Each of these animals had considerably different early histories, which can influence the development of vocal behavior. Animals which have been hand reared often exhibit slightly aberrant vocal behavior as adults (Epple, 1968). Further, they occasionally show a persistent tendency to exhibit juvenile vocal patterns, including a slight reduction in vocal activity (Moynihan, 1970).

The high frequency of vocalizations not clearly attributable to a particular animal, an artifact of a monaural monitoring system, implies that the data concerning sex related differences in response to the treatments should be viewed with caution. In fact, based on the results presented here, no statement regarding sex related differences in response to the treatments can be confidently proposed.

Under conditions featuring the vocalizations of *S. o. geoffroyi*, the magnitudes of the treatment effects could reasonably have been expected to be less than for those featuring the vocalizations of conspecifics, though the data do not support this contention. The total number of intervals during which vocalizations occurred under the three conditions featuring vocalizations of *S. o. oedipus* was 204, while under the four conditions featuring vocalizations of *S. o. geoffroyi*, the total was 269. Considering that there were unequal samples represented, a direct comparison of scores is inconclusive. Nonetheless, the highest response under any condition was observed under condition one, which features "F" chirps and partial "F" chirp trills of captive *S. o. oedipus,* where the male vocalized in seven intervals. Whether or not there is a differential responsiveness to the vocalizations of congeners compared to conspecifics is difficult to determine from these data.

Saddleback tamarins (*S. fuscicolis*) of four closely related subspecies exhibit differential rates of vocal responsiveness to vocalizations from animals other than conspecifics. A significant change in only one structural parameter of a territorial long call enabled animals to distinguish members of one subspecies from another (Hodun, Snowdon, & Soini, 1981). Snowdon and Hodun (1985) reported that individual mustache tamarins (*Saguinus mystax*) were able to identify an animal as being a troop member or not based exclusively on the presentation of territorial long calls. In fact, several sympatric Saguinus species, including saddleback tamarins (*S. fuscicolis*), emperor tamarins (*S. imperator*), and mustache tamarins (*S. Mystax*) are mutually responsive to one another's long calls. Epple (1968) reported that saddleback tamarins and cotton-top tamarins, responded in functionally appropriate ways to the vocalizations of common marmosets. Both Epple (1968) and Moody and Menzel (1976) found that cotton-top tamarins responded in kind to the "loud long calls" of saddleback tamarins. Further, the "long whistles" of Geoffroy's tamarins elicit functionally equivalent calls in response from saddleback tamarins (Moynihan, 1970). The same interspecific responsiveness probably exists between *S. o. geoffroyi* and *S. o. oedipus* with regard to long calls (Snowdon & Hodun, 1985), and other classes of vocalizations (Epple, 1968).

In fact, there were few significant differences in the number of intervals during which vocalizations were recorded for unidentifiable animals under conditions featuring vocalizations of *S. o. oedipus* when compared to those featuring vocalizations of *S. o. geoffroyi*. For example, the total number of intervals during which vocalizations were recorded for unidentified animals included 85 intervals for treatment 1, 81 intervals for treatment 2, 83 intervals for treatment 4, 68 intervals for treatment 5, 57 intervals for treatment 6, 35 intervals for treatment 7, and 20 intervals for treatment 8. Treatments 1, 5, and 7 featured the vocalizations of *S. o. oedipus*; while treatments 2, 4, 6, and 8 featured vocalizations of *S. o. geoffroyi*. The only obvious trend was the gradually decreasing frequency of daily intervals during which vocalizations occurred, an artifact of reduced sampling during afternoons. These data suggest that the subjects did not respond at lower rates to the vocalizations of *S. o. geoffroyi*, although the sample size is insufficient to support this contention with confidence.

Cotton-top tamarins respond differently to the calls of troop members than they do to those of unfamiliar animals (Cleveland & Snowdon, 1982; French & Snowdon, 1981). In fact, they can often recognize individuals based entirely on the uniqueness of vocal morphology--even in the absence of visual or olfactory cues (Snowdon, Cleveland, & French, 1983).

The long calls *of S. o. oedipus* and *S. o. geoffroyi* are morphologically distinct from those of Amazonian tamarins, which inhabit more humid environments. Their long calls possess morphologies which enhance their propagation in the more temperate habitats of

Panama and Colombia (Waser & Brown, 1986). At least with regard to these calls, their vocalizations are more convergent than those of other congeners. Subjectively, the vocalizations of Geoffroy's tamarins are higher in frequency, and more rapidly modulated than those of cotton-top tamarins. Unfortunately, at the time of this writing, no direct comparison of the vocal morphologies of these two species has been published.

The frequency of vocal activity shows a diurnal cyclicity. Vocalizations are less likely to be produced during the early morning, immediately following arising, and immediately prior to returning to the nest box in the evening (Caine, 1984: Neyman, 1978). During the course of this study, the greatest number of vocalizations were recorded during the late morning and the early afternoon. Although few data were collected between 06:00 and 09:00, recordings made during this time period feature few vocalizations. There was a bi-modal distribution in the scores for vocal activity, with peaks between 10:30 and 11:30 each morning, and another between 14:00 and 14:30 in the afternoon. Caine (1984) reported that, in captive *S. labiatus*, there was a bout of vocal activity in the early morning, after the tamarins had fully recovered from their nocturnal torpor. Waser and Brown (1986) contend that territorial vocalizations are more efficiently transmitted in the early morning, when there is less ambient environmental masking noise. Many forest dwelling animals emit territorial calls in the morning, prior to the inception of higher levels of insect and vegetative noise, increasing the effectiveness of their transmission. This finding was not supported by the temporal patterning of vocal activity observed in the subjects, possibly an artifact of reduced sampling during the morning hours.

The midmorning increase in vocal activity occurred shortly after feeding, and consisted primarily of quiet long calls and "C" chirps. "C" chirps are associated with food related situations (Cleveland & Snowdon, 1982). There was no convincing explanation for the slight increase in the rate of vocalization during the afternoons. This slight increase in vocal activity usually occurred around 16:30 hours, immediately preceding the closing of the zoo and was especially noticeable because it was followed by a quiescent period preceding retirement, a pattern also reported in red-bellied tamarins (Caine, 1984). Of possible significance was the observation that the mid-afternoon peak in vocal activity coincided with a predictable volley of "roar choruses" emitted by an adjacent pair of ruffed lemurs (*Varecia variegata*) which occurred around 14:30 almost daily. Whether or not the tamarins were responding to these pervasive sounds is not clear, but the nearly simultaneous increase in their rate of vocal activity is suggestive. During a 1981 study of the vocal interaction between two groups of siamangs (*Symphalangus syndactylus*) at the San Francisco Zoo, it was discovered that one of the most reliable predictors of an impending loud call chorus was an increase in vocalizations by a male chimpanzee (Tromborg, unpublished). In each instance, the vocal behavior of one species of primate was influenced by that of another, a type of interaction that might occur regularly in zoos.

The suggestion that vocalizations, especially those of conspecifics, can function as reinforcers of vocal behavior was obtained from the research of Haraway and Maples (1981), who reported that captive siamangs (*Symphalangus syndactylus*) became more vocally active when presented with the loud calls of conspecifics. The increased rate of vocal activity was reported to persist in the absence of treatments, suggesting that the performance of vocal behavior was intrinsically reinforcing. This might parallel the finding that the subjects of this study produced low level vocalizations continuously throughout the study, even in the absence of treatments.

A partial analysis of the continuous recordings made of the tamarin vocalizations suggests that the most commonly recorded vocalization throughout the study was the "C" chirp. These were not primary components of treatment variables, yet they were emitted at any time of the day, for extended periods of time, with irregular durations and inter-call intervals. These are usually emitted antiphonally in food related situations or within the context of low level foraging. The constant presence of ad libitum food and the constant, low level of foraging are probably associated with the high emission rate of "C" chirps. Epple (1968), reported that the most frequently recorded vocalization in her colony of cotton-top tamarins was a short duration, monosyllabic contact call, suggesting that it might have been the "C" chirp, described by Cleveland and Snowdon (1982).

Based on the work of Cleveland and Snowdon (1982) and Wolters (1978), it is reasonable to conclude that most of the short duration, low-level contact calls were emitted by the female, while most of the longer, higher amplitude territorial calls were emitted by the male, though precise attribution of response is difficult.

Epple (1968) reported that captive tamarins emitted fewer vocalizations than their free living counterparts. In the absence of appropriate visual referents, many primates will either not respond to acoustic stimuli, or will rapidly habituate to them (Redican, 1975).

This is even true with predator warning calls. Goeldi's monkeys exhibited reduced responses to predator warning calls when the predator was not visible, though their responses increased when the stimulus animal could be seen (Masataka, 1983).

Erkert, *et al.*, (1986) have reported that social masking of activity levels occurs in response to vocalizations from other animals in the vicinity of captive groups of common marmosets. This masking can dampen the normal circadian rhythmicity in activity cycles characteristic of crepuscular species. Consequently, the vocal activity of other zoo animals, especially those with vocalizations featuring morphologies similar to those of tamarins, might have influenced the levels of vocal activity observed in the subjects.

Terborgh (1983) reports that groups of *S. imperator* and *S. fuscicolis* form interspecific associations and that the animals employ interspecific vocalizations to coordinate their foraging activities. The subjects were in acoustic contact with a nearby group of emperor tamarins, and could have been influenced by this contact.

The ontogeny of vocal behavior in several primates has been investigated and found to be influenced by social experience (Newman & Symmes, 1982; Snowdon 1978). Cotton-top tamarins, for example, show a pattern of vocal development observed in primates that demonstrate vocal learning, implying that early social experience could have influenced their vocal competency as adults. The subjects used in this study had different backgrounds as infants. The female was reared with other tamarins, while the male was hand reared. Different experiential factors could account for differences in the respective abilities of the subjects to recognize and respond appropriately to the playback variables.

The vocal behavior of animals serving as subjects in playback studies is also influenced by their social environments. Epple (1968) reported that individually housed tamarins exhibited reduced rates of vocal activity compared to those housed together in pairs. It is conceivable that animals not in acoustic contact with other groups of related animals might exhibit a reduction in territorial calling, while those groups not containing infants might exhibit a reduction in intratroop vocalizations.

One category of calls that appears to have been under represented in the playback treatments were contact calls. These calls almost always elicit the emission of similar vocalizations in response (Cleveland & Snowdon, 1982; Epple, 1968). Whether or not the elements of the vocalizations of Geoffroy's tamarins which resembled "C" chirps were treated as contact calls is not clear. However, Epple

(1968), reported that if the mobbing calls (Tsk calls) of common marmosets were administered to other Callitrichids, heterospecific animals, would respond in kind, often for periods of up to 15 minutes.

An important consideration in the design of sound playback studies is the sound pressure level at which treatments are administered. Treatments administered at insufficient levels might elicit few responses, while those administered at excessive levels can actually harm subjects (Gamble, 1982). The treatment variables employed herein were presented at levels commensurate with those suggested by other researchers conducting similar studies, ranging between 67 dB and 72 dB (Green, 1975; Masataka, 1983; Newman & Symmes, 1982). Consequently, inappropriate sound pressure level should not have been a factor in the observed rates of response recorded during the study. The use of a single channel monitoring system made the attribution of vocal responses to a specific animal particularly difficult. When the numbers of vocalizations attributed to either subject are summed and compared, all are significant, yet they represent only a fraction of the total number of responses. When the category for unidentifiable animals is included in the analysis, the frequency of intervals during which vocalizations were recorded increases significantly. Problems concerned with precisely identifying a respondent are not unusual in the study of primate vocal behavior (Byrne, 1981; 1982). These shortcomings can be addressed by the use of multi-channel monitoring systems or by the use of telemetering devices (Mackay, 1970).

Epple (1968) claims that a human observer cannot detect the differences between the calls of *S. o. oedipus* and *S. o. geoffroyi*. Based on subjective comparisons of recordings of the two subspecies, some might not agree with this statement. The vocalizations of *S. o. geoffroyi* sound more complex and appear to have a somewhat higher fundamental frequency than those of *S. o. oedipus*. These differences could be artifacts of the different group compositions of the animals from which the treatment recordings were made, or could be artifacts of poorly matched recording and playback equipment. In fact, poorly matched equipment could have influenced the response of the subjects by degrading the apparent quality of the program material employed in the treatments. To the extent that program material diverges from the original material, it could become less relevant to the subjects (Wiley & Richards, 1978). High frequency attenuation, improper amplitude, absent phase information, inaccurate or variable pitch, and inappropriate point sources all can reduce the efficacy of acoustic treatment variables. Sufficient degradation could result in the program material being perceived as obtrusive noise, completely negating its usefulness in an experimental protocol and, possibly introducing a stressor to the subjects (Gamble, 1982).

Nonetheless, the usefulness of acoustic treatments featuring the vocalizations of conspecifics and congeners for influencing the rate of vocal behavior in captive tamarins is suggested by the increase in this measure under treatments. Factors influencing the effectiveness of the treatments include function of the vocal signal, age and sex of respondents, absence of extraneous sound sources, and the amplitude and accuracy of the recorded treatments.

Scanning

When the baseline scores are compared to the combined treatment and intertreatment scores, scanning significantly decreases with treatments ($\chi^2 = 111.93$, $\underline{n} = 2425$, $\underline{df}$ 1 , $\underline{p} <.001$).

When conditions 3 and 3' are compared, scanning significantly increases with treatments ($\chi^2 = 8.79$, $\underline{n} = 173$, $\underline{df} = 1$, $\underline{p} <.05$).

The hypothesis tested with this measure states that the frequency of scanning should significantly increase when the subjects are presented with any of the eight treatments, particularly under conditions 5 and 7, which feature calls associated with territorial defense (French & Snowdon, 1981).

While there is a significant change in the frequency of scanning, the directionality of the change is the opposite of what was predicted for all comparisons except for that between conditions 3 and 3'. During the baseline, the male scanned during 829 intervals, while the female scanned during 650 intervals. When the conditions were combined, the male scanned during 607 intervals, while the female scanned during 447 intervals. Scanning was much higher under condition 3 than under condition 3', with the male scanning during 71 intervals and the female scanning during 42 intervals under condition 3, while the male scanned during 43 intervals and the female scanned during 24 intervals under condition 3'. There was a pronounced sex difference in the rate of scanning, with the male almost always scanning more than the female. The positive change in scanning under condition 3 was reasonable, for cicadas are a prime prey item for wild tamarins. It was conceivable that the animals were engaging in a type of prey detection when these sounds were administered. Since the recording was that of a chorus of insects, and not of a single organism, the animals might have been engaging in scanning in an attempt to visually locate a prey object, or several of them, on which they could not obtain a precise auditory fix. The remainder of the results were unexpected. The reduction in scanning can possibly be attributed to habituation effects (Caine, 1983). It was possible that the continual exposure of the tamarins to formerly arousing phenomena resulted in a decline in reactivity to these stimuli.

Part of the rationale for including this measure in this study was to determine if the levels of some territorial monitoring behaviors could be regulated by the provision of traditionally arousing or salient acoustic phenomena. The zoo environment is not a completely benign habitat. There are threatening aspects to captive environments, including the chronic exposure of animals to sounds and odors of traditional ecological adversaries, including humans. It is conceivable that animals housed in captivity for extended periods or those born in captivity might exhibit fewer vigilance behaviors than wild conspecifics. While the zoo features many potentially arousing acoustic and visual aspects, including the sounds and smells of potentially dangerous species (Caine, 1984), the precise interaction between changes in the acoustic habitat and rates of scanning are not well documented.

The influence of the treatments on the rate of scanning is difficult to separate from other factors that might influence changes in its frequency of occurrence. The rate of scanning was strongly dependent on the time of day that observations were conducted. Tamarins exhibit a crepuscular activity pattern (Dawson, 1979) and show peaks in the frequency of scanning in the early morning, just after leaving their nest box, and again in the evening, immediately before returning to it (Caine, 1984). Scanning was usually directed toward portions of the surroundings from which threatening stimuli had originated in the past. All vertical levels of the surroundings were usually scanned at equivalent rates. Less relevant stimuli appeared not to significantly influence the rate of scanning.

Since scanning is thought to function both as an antipredator detection behavior and as a means of detecting prey, scanning might occur at a relatively high baseline rate in the absence of any external stimuli. This appears to have been the case in this study, where the rate of scanning during the baseline study was actually higher than under the treatment conditions. It is conceivable that the slightly lower level of scanning observed under the treatment conditions was a result of the animals having become habituated to their enclosure and to other formerly arousing cyclical phenomena in their immediate surroundings, irrespective of the treatment conditions. This possibility introduces a confounding element into this project.

The subjects had only recently been introduced into their enclosure at the onset of the baseline study. Prior to this introduction, they had been housed in a relatively predictable habitat in the zoo nursery. Consequently, the baseline levels of scanning might have been artificially high as the tamarins surveyed their novel surroundings. Scanning occurs at relatively high levels in animals which have only recently been introduced into new enclosures (Caine, 1984).

It is also conceivable that the tamarins were responding to acoustic phenomena other than the treatments. Scanning is preferentially performed in response to the perception of novel visual phenomena within or near enclosures (Caine, 1984). Hence, the high levels of scanning recorded during the baseline, and perhaps some of the variability in scanning observed under some treatment conditions could have been prompted by factors other than those being manipulated, including low level sounds from other enclosures and novel visual stimuli.

One difficulty in recording the occurrence of scanning is that it is similar to some other environmental monitoring behaviors performed by Callitrichids and is difficult to differentiate from them. Vogt (1978) reports that captive saddleback tamarins assume an upright posture to monitor their surroundings, something that was not always the case with scanning in these subjects. Red bellied tamarins engage in at least two forms of environmental assessment, one of which is clearly scanning, involving a lateral sweep of the head and functions as a continuous, low level monitoring behavior (Caine, 1983;1984; Terborgh, 1983). There is also a more generalized surveillance or investigatory behavior which does not feature the continuous lateral rotation of the head, but involves head tilting or head cocking. Head tilting is thought to increase retinal disparity and is important in improving depth perception in animals with small interocular distances (Charles Snowdon, personal communication, 1986). Scanning is also difficult to distinguish from head tilting, a behavior that is more intimately associated with the expression of hostility than with surveillance (Moynihan, 1976).

In wild tamarins, scanning is not performed at equal rates by all members of a group. The role of "primary scanner" is assumed by different individuals throughout the day. This might represent a cooperative division of labor in the maintenance of anti-predator defense. This type of role reversal was not clearly visible during this study. The male usually scanned more frequently than the female, though under conditions 7 and 7', the female scanned during slightly more intervals than the male. These conditions feature a complex combination of the calls of captive cotton-top tamarins, and it is conceivable that the female perceived these as conspecifics and was attempting to locate the source of out-group vocalizations.

The degree of arousal of an animal that is scanning can be estimated by the degree of piloerection observed during the scan. When piloerection is noticeable, the animal is considered to be aroused and is probably scanning in response to some threatening phenomenon in its surroundings. Conversely, scanning or visual monitoring without piloerection indicate little arousal and could reflect curiosity (Menzel & Juno, 1985).

One aspect of scanning that has not been well investigated is its possible involvement in sound localization. Lateral displacement of the head, or triangulation, could enable an animal to determine the approximate location of a sound source. Separating the involvement of visual from the involvement of acoustic stimuli in modulating the rate of scanning is impossible, but the orientation of the head to localize sound must be considered as a likely occurrence. The ability to localize sound is an acquired skill and only slowly develops in young animals. In fact, the ability to correctly localize sounds only develops if animals are able to experience this activity (Newman & Symmes, 1982).

Scanning must be distinguished from other surveillance behaviors. Both scanning and other forms of visual surveillance are mechanisms for animals to assess the security of the immediate surroundings (Caine, 1984). The rate of scanning can be modified in some species by the presentation of potentially arousing acoustic stimuli. Seyfarth, et al, (1980) reported that, in response to the alarm calls of conspecifics, vervet monkeys increased their rates of scanning. French and Snowdon (1981) reported that cotton-top tamarins also increase their rates of scanning in response to the sight or vocalizations of an intruder. Scanning is also intimately associated with the frequency of foraging, a measure which occurred at relatively constant levels throughout this study. Neyman (1978) reported that wild cotton-top tamarins continuously scanned while foraging, a finding that these data to not clearly support.

The rate of scanning is also influenced by the presence of human observers and veterinary staff. Animals often exhibited increased rates of scanning in the presence of individuals wearing zoo uniforms and visitors wearing brightly colored clothing. The behavior of the subjects is suggestive of increased arousal and heightened vigilance. All of these extraneous factors probably occlude the effects of the treatments on the frequency of scanning.

It is conceivable that the rates of scanning are more amenable to modification through the presentation of visual stimuli than through the presentation of acoustic stimuli. This suggestion should be investigated so that the persistence of the performance of this important environmental monitoring behavior is encouraged in captivity, possibly a critical consideration if tamarins are ever to be re-introduced into the wild.

Display

When the baseline scores are compared to the combined treatment and intertreatment scores, displays significantly decrease with treatments ($\chi^2 = 70.42$, $\underline{n} = 142$, $\underline{df} = 1$, $\underline{p} <.001$).

The hypothesis tested with this measure states that the frequency of display behaviors should increase when the animals are exposed to treatments that feature the vocalizations of other troops of tamarins, i.e., all treatments except condition 3.

There was a pronounced sex difference in the number of intervals during which each animal displayed, with the female displaying during more than twice as many intervals as the male. During the baseline, the female displayed in 85 intervals, while the male displayed in 36. Under condition 6, the female displayed during one interval, while the male failed to respond; under condition 7, the female displayed under 4 intervals, while the male displayed under 2; and under condition 8, the female displayed during 3 intervals, while the male failed to respond. In fact, under all but one of the 17 conditions, the female displayed during more intervals than the male. The condition associated with the highest frequency of displaying was condition 7, a recording of captive cotton-top tamarins featuring vocalizations including "C chirps," "squeals," "descending multi-whistles," and a "partial long call chorus."

The significant decrease in the frequency of displaying is difficult to explain in view of the findings of Cleveland and Snowdon (1982), which suggest that tamarins will respond to out-group vocalizations by increasing the frequency of territorial displays. Conceivably, the low incidence of displaying can be attributed to the low salience of the treatments or to incomplete operational definitions. Displaying was operationally defined as featuring an erect bipedal stance with a frontal presentation of the genitals, a behavior rarely observed. Another form of display behavior features an erect bipedal stance, dorsal surface toward the target, and tail raised to expose the genitals, a behavior that was never observed. Both forms of display are more common in Callithrix species than in Saguinus species, and more common in males than in females (Omedes & Carroll, 1980).

Altmann (1967) states that displaying, in the form of genital presentation can indicate assertiveness or sexual receptivity on the part of one animal toward a conspecific. To the extent that this is true with genital displaying in tamarins, the treatments should have exerted little effect on the rate of displaying. To the extent that displaying is involved in territorial defense and defensive threat, the treatments should have been correlated with an increase in these behaviors.

French and Snowdon (1981) reported that male tamarins responded more than females to isosexual intruders with increases in genital displays. Cotton-top tamarins appear to be able to discriminate both the species and sex of intruders exclusively on the basis of vocalizations, and show dimorphic responses to these presentations. Both males and females respond more strongly to the presence of isosexual animals than to heterosexual animals. Whether or not the quality of the playback treatments was sufficiently high to allow the subjects to assess the species and sex of the vocalizing animal is not clear. The use of vocalizations from a closely related congener in 4 of the treatments could have been a factor in the relatively low magnitude of many of the effects. Although similar, the morphologies of the vocalizations of Geoffroy's tamarins might be sufficiently structurally distinct from those of cotton-top tamarins that they possess reduced functional significance. This is a tenuous argument, however, because the magnitudes of the treatment effects are not significantly different for treatments featuring the vocalizations of one species compared to the other. Another possible factor mitigating the responsiveness of the subjects is the finding by Redican (1975) that some primates exhibit reduced rates of response to the presentation of acoustic stimuli in the absence of accompanying visual referents. This suggests that differential responsiveness to animals of different species and sexes can be investigated through the artificial manipulation of group composition. When cotton-top tamarins were introduced to red bellied tamarins they responded less strongly than they did to the presence of strange conspecifics (Epple, 1968). The response was dimorphic, with females exhibiting increased rates of scent marking while males exhibited increased threats to attack (French & Snowdon, 1981). Males threatened males more than they threatened females, while females threatened both sexes equally.

Both sexes, appeared to be able to discriminate the sex and species of the unfamiliar animal. Males typically respond to intruders with a greater intensity than females, as measured by a greater degree of piloerection. The greater degree of arousal exhibited by males suggests that they are more likely to engage in interactions at territorial boundaries than females, who are apparently more involved with intratroop social dynamics (Welker and Luhrmann, 1978). This same type of dimorphic response has been observed in the closely related Geoffroy's tamarin, in which males perform the majority of genital displays (Dawson, 1979). Reduced aggression between heterosexual adults and between females could function in free living animals to facilitate the acceptance of immigrating females, into newly established groups, a mechanism that could facilitate the maintenance of genetic diversity (Neyman, 1978).

The contention that response to acoustic stimuli is enhanced if visual stimuli are simultaneously presented is probably less true for Callitrichids, inhabitants of dense forest habitats wherein visual signals are inhibited. Consequently, the absence of accompanying visual stimuli should not have dampened the response of the subjects.

The presence of infants can influence the types and frequencies of displaying. Wolters (1978) reports that in the presence of infants, males become more aggressive toward all intruders, regardless of sex and species. The data do not suggest that there was any increase in the rate of scent marking during the periods of time circumscribing the births of infants. Further, the young did not survive long enough for this contention to be adequately tested.

The frequency of genital displays in cotton-top tamarins is thought to be somewhat lower than those for other Callitrichids (Wendt, 1979), though this finding has not been corroborated by other researchers. The results presented here tend to support this contention. Though genital displays were extremely rare, they were sufficiently novel that few were likely to have been missed by trained observers.

The low rate of genital displays recorded throughout this study are insufficient to support the contention that purely acoustic treatments can modulate the rate of scent marking in captive tamarins. Future research should emphasize the use of multi-modal conditions and should address the issues of changing compositions of the study group and of inadequate operational definitions.

Scent Marking

When the baseline scores are compared to the combined treatment and intertreatment scores, there was no significant change in the frequency of scent marking ($\chi^2 = .26$, n = 32, df = 1).

The hypothesis tested with this measure states that the frequency of scent marking should increase when the animals are exposed to 7 of the treatments, especially those featuring the long calls of other tamarins, e.g., treatments 5 and 7 (Cleveland & Snowdon, 1982; Epple, 1968; Kleiman, 1978).

Not only were there no significant changes in the frequency of scent marking throughout the course of the study, but there were no significant differences in the frequency of scent marking when the treatment condition or sex of the respondent was considered. The numbers of intervals during which scent marking was observed were extremely low, with the male scent marking during 6 intervals and the female during 13 intervals throughout the baseline. Under all of the combined treatment conditions, the male scent marked during 7 intervals while the female marked during 3. This is surprising in view of the research of Cleveland and Snowdon (1982) which found that tamarins will increase their rates of scent marking in response to the long calls of strange cotton-top tamarins. Elements of long calls are present in conditions 5 and 7.

Most male mammals scent mark considerably more than females. In most Callitrichids, however, females mark more than males (Box & Morris, 1980); Epple, 1976; 1985; French & Snowdon, 1981; Omedes and Carroll, 1980). In a study of four pairs of the common marmoset the males marked 1361 times compared to 2102 times for the females (Sutcliffe & Poole, 1978). Female cotton-top tamarins usually scent mark significantly more frequently than males (French & Cleveland, 1984).

In response to a perceived intruder, female cotton-top tamarins have been reported to increase rates of super-pubic scent marking, while males typically exhibit no increase in scent marking but show an increase in the number of genital displays (French & Snowdon, 1981). Female cotton-top tamarins can mark as often as one time every 20 minutes in response to extraneous stimuli, especially when they are not in the presence of a dominant female (French, et al., 1984).

This measure was meant to investigate the influence of potentially arousing acoustic phenomena on the rates of super-pubic and sternal scent marking, though ano-genital scent marking was emphasized. The rates of sternal marking were so low that this behavior was virtually never observed. This finding supports the contention of Omedes and Carroll (1980) that this is an extremely rare behavior. In the absence of other adults, the low rates of scent marking were not entirely unexpected.

In common marmosets, both the development of glandular fields and the rates of scent marking are enhanced in dominant animals in the presence of subordinate animals (Sutcliffe & Poole, 1978).

Sex based differences in response to the treatments are also not surprising. Females tend to respond to the sounds of unfamiliar animals with increased scent marking, while males do not (French & Cleveland, 1984). Unfortunately, there is considerable variability in response even between individuals; in common marmosets there can be greater variability than that based on sex (Sutcliff & Poole, 1978). Further, these dimorphic tendencies do not extend across the family. Kleiman (1978) reports that there are virtually no sex differences in scent marking in golden lion tamarins in response to the sounds of unfamiliar animals. The dimorphic nature of scent marking is dependent on the particular class of marking under consideration. Because observers were instructed to concentrate on the more easily observed ano-genital form of scent marking, the frequencies of super-pubic and sternal marking were probably underestimated. Oddly, this procedure should have skewed the results toward greater scent marking frequencies for the female compared to the male, a finding which the data do not support. Within the Callitrichidae, there is little sexual dimorphism in the rates of muzzle rubbing, urination, and defecation, often considered scent marking behaviors (Sutcliffe & Poole, 1978) However, when compared to males, most female Callitrichids exhibit higher rates of ano-genital scent marking (Cleveland & Snowdon, 1984). Male cotton-top tamarins exhibit a greater increase in the rate of sternal scent marking compared to females while females exhibit a greater increase in the rate of ano-genital marking in response to the perceived presence of unfamiliar animals (French & Snowdon, 1981).

There are profound developmental influences on the frequencies of all types of scent marking behavior. All types of scent marking are low in very young animals, increasing to their adult values at around two years of age. The subjects of this study were mature at the onset of the research and should have exhibited rates of scent marking typical for adult conspecifics.

Ano-genital marking, specifically, is associated with changes in the reproductive state of the female, increasing during peak receptivity, facilitating assessment of this condition by the male. In large colonies of tamarins, scent marking has been implicated in the suppression of cyclicity in subdominant females (French, et al., 1984; Kleiman, 1978). The relatively young age of the subjects, and the absence of other adult animals possibly accounts for the relatively low rate of scent marking throughout the study. Epple (1985) reported that scent marking frequencies increase in the presence of other scent marks deposited by unfamiliar animals, again a factor that could partially account for the low rate of scent marking by the subjects.

The finding that super-pubic scent marking functions primarily in agonistic and territorial interactions implies that it might occur at relatively low frequencies in the absence of other groups of adult conspecifics (Wolters, 1978). The absence of other adult tamarins in the immediate vicinity of the subjects could partially explain the relatively low rates of both super-pubic and sternal scent marking by the subjects.

The relatively low rate of super pubic scent marking might also imply that the subjects were not responding to the treatments as if they suggested the presence of unfamiliar conspecifics. French and Snowdon (1981) reported that cotton-top tamarins are able to assess the species of a perceived intruder exclusively on the basis of vocalizations, and that they exhibit a reduced response to the vocalizations of congeners compared to conspecifics. Treatments featuring the vocalizations of Geoffroy's tamarins could have exerted a reduced effect on the subjects compared to treatments featuring the vocalizations of cotton-top tamarins. This contention is supported by research that suggests that adult tamarins respond most strongly to the vocalizations of isosexual conspecifics (Epple, 1978).

The subjects often performed scent marking while foraging. Scent marking, especially muzzle rubbing, is especially difficult to observe when animals are performing investigatory behaviors with their muzzles. This difficulty probably resulted in large numbers of scent marking behaviors not being recorded. In fact, the subtle nature of the locomotor patterns involved with scent marking implies that many episodes of scent marking were missed by observers.

Scent marking frequencies are highest when animals are first introduced into new enclosures (Epple, 1975). The finding that scent marking frequencies did not decline throughout the course of the study suggests that the subjects could have been displaying elevated rates of scent marking at the onset of the study in response to having only recently been placed into their enclosure, while the persistence of low levels of marking could have indicated that the animals were well habituated to their surroundings.

Scent marking is one measure that is severely affected by husbandry routines. Hediger (1950/1964) discussed the importance of olfaction in captive settings as providing a means for animals to maintain the familiarity of their habitats through ritual scent marking. He wrote of animals regularly visiting sites of demarcation and of keepers regularly cleansing them. This conflict can introduce a confounding element into studies of scent marking behavior, with the rates of scent marking being elevated as animals reanoint their surroundings after cleaning by caretakers. Epple (1975) and Hampton, *et al.* (1966) have reported that all Callitrichids will increase their rates of scent marking after the enclosure has been cleaned.

Another potentially severe confounding factor associated with this measure is that the frequency of scent marking is intimately related to the reproductive cycle of the female (French, 1982). Scent marking increases dramatically during the periovulatory period of the reproductive cycle (Epple, 1975). This could potentially obscure any change in scent marking frequency associated with the treatments. The frequency of scent marking has also been correlated with the level of arousal in Callitrichids (Epple, 1975). If the intrusion of keepers into the enclosure or inappropriate visitor behavior functioned as stressors, then either of these phenomena could have modulated the rate of scent marking, again obscuring the influence of the treatments.

The frequency of scent marking can also be influenced by the introduction of novel objects into the enclosure (Coates & Poole, 1983). Box & Morris, 1980) report that most female Callitrichids engage in the scent marking of novel objects more than males. Kleiman (1977) and Sutcliffe and Poole (1978), however, report that in golden lion tamarins and common marmosets respectively, males engage in this type of scent marking more than females. This disagreement probably arises from the failure of the respective researchers to clearly identify the stimulus eliciting the change in scent marking frequency or from inadequate operational definitions of scent marking.

The playback variables exert some influence on the frequency of scent marking. French and Snowdon (1981) reported that cotton-top tamarins exhibited a dimorphic response to the playback of territorial long calls. Long calls were components of only two conditions, 5 and 7. Even under these conditions, however, there was no significant change in the rate of scent marking. The absence of significant treatment effects suggests that the selection of playback variables did not include those that would have elicited the greatest response from the subjects.

One consideration that was overlooked at the onset of this study was the proximity of other closely related animals. The enclosure housing the subjects was connected via air ducts to a nearby enclosure housing a group of emperor tamarins. It is conceivable that the two groups of tamarins were in olfactory contact with one another. What effect this had on the rate of scent marking by the subjects is not clear, though it is reasonable to suggest that it could have dampened the effectiveness of the treatments by elevating the basal level of territorial scent marking, though the low level of marking also might suggest habituation to the other group of tamarins.

Although the treatments appeared to exert little influence on the rate of scent marking, the subtlety of this behavior also makes it difficult to observe and many episodes of marking, especially those associated with foraging, were not scored. Further, incomplete or confusing operational definitions probably contributed to the low reliability of this category of behavior. If the frequencies of scent marking behavior are to be manipulated, the most effective method is probably through the application of olfactory treatments. Even more interesting research might revolve around the influence on behavior exerted by the presentation of multi-modal signals, the form that messages usually take in nature.

Sexual Behavior

When the baseline scores are compared to the combined treatment and intertreatment scores, sexual behavior significantly decreases with treatments ($\chi^2 = 4.9$, $\underline{n} = 59$, $\underline{df} = 1$, $\underline{p} <.05$).

When the scores for conditions 3 and 3' are compared, sexual behavior significantly increases with treatments ($\chi^2 = 6.0$, $\underline{n} = 6$, $\underline{df} = 1$, $\underline{p} <.05$).

When the scores for conditions 4 and 4' are compared, sexual behavior significantly decreases with treatments ($\chi^2 = 4.0$, $\underline{n} = 4$, $\underline{df} = 1$, $\underline{p} <.05$).

The hypothesis tested with this measure states that the frequency of sexual behavior should not significantly change when the animals are exposed to the treatments.

There is a strong directionality in the scores for sexual behavior, with the male performing these behaviors more than twice as frequently as the female. During the baseline, the male engaged in sexual behavior during 23 intervals, while the female engaged in sexual behavior during 16. Throughout the combined treatment period, the male engaged in sexual behavior during 15 intervals, while the female engaged in sexual behavior during 5 intervals. When the scores for condition 3 are compared to those for the following intertreatment interval, sexual behavior increases. The male engaged in sexual behavior during 4 intervals while the female engaged in sexual behavior during two intervals. Under condition 3' there was no observed sexual behavior (χ^2=6.0, p <.05). When the scores for conditions 4 and 4' are compared, sexual behavior declines. Under condition 4 there is no observed sexual behavior, while under condition 4', the animals were observed to engage in sexual behavior in two intervals each (χ^2=4.0, p <.05).

These are extremely low values for this measure, making conclusions regarding the influence of the treatments speculative. Condition 3 consists of a cicada chorus and was hypothesized to have little influence on behavior, especially vigilance activities. To the extent that the animals were not aroused by this treatment, there should have been little influence on their behavior, including maintenance and reproductive behaviors. It is extremely doubtful that there is any facilitation of reproductive behavior attributable to this treatment.

Conversely, treatment 4 is a complex recording of several wild Geoffroy's tamarins engaging in relatively relaxed social behavior. It is conceivable that a reduction in sexual behavior could be attributed to increased vigilance behaviors, including scanning. To the extent that animals are subjected to sounds that increase stress or levels of arousal, the occurrence of reproductive behavior can be negatively impacted by sound (Gamble, 1982). While it is possible that this is what occurred under condition 4, it is more likely that these results are spurious. The number of intervals during which copulatory behavior was observed is too low to allow any conclusive statements to be made regarding the hypothesized influence of the treatments.

Factors other than the possible influence of the treatments could have influenced the frequency of sexual behavior. For example, the frequency of copulations is strongly influenced by the degree of familiarity between the animals (Snowdon, 1990). The reduction in sexual behavior observed in the subjects could have been an artifact of the maturation of their pair bond. When male and female Callitrichids are first introduced to one another, there is an initially high rate of copulatory behavior, which declines as the relationship matures (Snowdon, 1990; Sutcliff & Poole, 1978). The greatest number of copulations were observed in October and November of 1985. This was the period of time encompassed by the baseline component of the study. The subjects had been housed together in their enclosure for approximately 5 months, suggesting that they had formed a mature pair bond. Hence, this copulatory behavior was not a result of a recent introduction, but rather represented receptivity on the part of the female. The timing of this increase in reproductive behavior corresponded well with the peaks in copulatory behavior reported for wild tamarins (Hershkovitz, 1977). This peak in copulatory activity ensures that young tamarins are born in April and May, periods of time during which there is an increase in food availability in Colombia.

Perhaps the most important finding obtained with this measure was that acoustic enrichment schemes, if relatively well designed, should not negatively influence reproductive behavior in tamarins. Hence, to the extent that acoustic enrichment schemes improve other dimensions of the habitats of captive primates, there need be little concern for negatively affecting reproductive success.

Allogrooming

When the baseline scores are compared to the combined treatment and intertreatment scores, allogrooming significantly decreases with treatments ($\chi^2 = 27.86$, $\underline{n} = 942$, $\underline{df} = 1$, $\underline{p} < .001$). When the scores for conditions 2 and 2' are compared, allogrooming significantly increases with treatments ($\chi^2 = 13.76$, $\underline{n} = 5$, $\underline{df} = 1$, $\underline{p} < .05$).

When the scores for conditions 3 and 3' are compared, allogrooming significantly decreases with treatments ($\chi^2 = 4.09$, $\underline{n} = 55$, $\underline{df} = 1$, $\underline{p} < .05$).

The hypothesis tested with this measure states that the frequency of allogrooming should decrease when the animals are exposed to all treatments. When the baseline scores are compared to the combined scores for all treatments, there was no significant change in the number of intervals during which the male groomed the female.

The male groomed the female during 378 intervals during the baseline compared to 355 intervals under all 16 conditions. The number of intervals during which the female groomed the male declined significantly, decreasing from the baseline total of 174 intervals to the total for the combined conditions of 72 intervals. There is a pronounced directionality in allogrooming, with the male grooming the female in more than twice as many intervals as the female groomed the male. This pattern persisted throughout the baseline and during all 16 conditions. Of the few significant results obtained when comparing treatment intervals and intertreatment intervals, there was a significant difference between the combined scores for the two animals under condition two (recordings of *Saguinus o. geoffroyi*), and the following intertreatment interval, with allogrooming significantly declining during the intertreatment interval. During condition 2, the male groomed the female in 45 intervals while the female groomed the male in 17 intervals. Under condition 2' the male groomed the female in 19 intervals while the female groomed the male in 8 intervals. This finding implies that the frequency of male grooming of the female during the presentation of treatment 2 was high, though not necessarily in response to the treatment. Conversely, the decline in the rate of the male grooming the female could have been in response to the introduction of the treatment. This recording features a complex combination of calls, produced by a troop of wild Geoffroy's tamarins. Qualitatively, the calls resemble "A chirps," "G chirps." "small, initially modulated whistles," and "B trills" of cotton-top tamarins. While the source group vocalized, they engaged in scent marking and foraging. It is conceivable that this treatment did not feature any vocal components that typically elicit territorial or vigilance behaviors; minimally it appears not to have been arousing. Essentially, this treatment introduces the subjects to sounds of similar animals engaging in relaxed social interactions. The decline in the rate of allogrooming during the following intertreatment intervals suggests that the effect was immediate.

The other significant comparison occurs between condition 3, a recording of a cicada chorus, and the following intertreatment interval, during which allogrooming of the female by the male significantly increases. Under condition 3, the male groomed the female during 19 intervals while the female groomed the male during only 1. Under condition 3', the male groomed the female during 32 intervals while the female groomed the male during 3. It is conceivable that treatment 3 is more reminiscent of low level, environmentally relevant sounds than the other treatment conditions and might be functioning to mask unnatural ambient sounds. The reduction in allogrooming was not expected in view of the proposed effects of this treatment, which included increases in the rates of allogrooming and environmental exploration. It is conceivable that the rate of allogrooming declined as the animals engaged in more episodes of scanning and environmental exploration, possibly to locate insect prey.

Another unexpected result, one with potentially valuable implications, involves the higher rates of allogrooming under all conditions featuring the complex vocalizations of wild *S. o. geoffroyi* when compared to the rates of allogrooming under conditions featuring the vocalizations of captive *S. o. oedipus*. Under all 4 conditions featuring wild tamarins, the rates of allogrooming were slightly higher. This suggests that the introduction of low level acoustic treatments featuring the sounds of animals engaging in social interactions might be useful in encouraging social interactions in captive animals that are confronted with disruptive environmental conditions on a regular basis. The magnitude of the effects was not large, but the trend is consistent across all treatment conditions.

The remainder of the findings were exactly the opposite of the trend observed in most cercopithecines and some other tamarins, where females groom males more than males groom females (Box & Morris, 1980; Sparks, 1969).

In a comparative study of Callitrichids, Omedes and Carroll (1980) reported that in cotton-top tamarins, females groomed males more than males groomed females, while in the red-handed tamarin and the red-bellied tamarin, males groomed females more than females groomed males. In one study of grooming in cotton-top tamarins, Welker and Lurhmann (1978) reported that males groomed females more than females groomed males, while in another, the opposite results were obtained (Welker and Luhrmann, 1978).

Vogt (1978) reported that in saddleback tamarins housed in a semi-natural habitat, social grooming was the most frequently observed social interaction, occurring in 36% of all observation intervals and comprising 26% of all social behaviors. Price and Hannah (1983) reported that, in a comparative study of cotton-top tamarins and golden lion tamarins, differences in the rates of allogrooming were based on individual variation more than on species or sex based differences.

The sampling method employed in the current study precludes any time budget analysis, but allogrooming was the most frequently observed social behavior. In common marmosets, the rate of allogrooming is dependent on the length of time that animals have spent together, with the male grooming the female more than the female grooms the male. In fact, males typically exhibit more affectional behavior of all types compared to females (Epple, 1976; Woodcock, 1982). This effect is even more pronounced if the subjects have only recently been introduced to one another. There is a gradual decline in the rate of allogrooming as the pair bond matures, possibly representing the habituation of the animals to one another. Grooming frequencies are also influenced by social factors other than the maturity of the pair bond. Young tamarins exhibit elevated rates of grooming when housed exclusively in pairs or in small social groups (Price & Hannah, 1983; Neyman, 1978). During the course of this study, the frequency of allogrooming declined during the afternoons. Although this could have been a result of the subjects habituating to one another, it was probably an artifact of the reduced number of afternoon sampling intervals.

Behavioral enrichment strategies are often conceived with the goal of influencing the behavior of captive animals in ways that enable them to engage in activities similar to those of free living conspecifics. The decline in the rate of allogrooming obtained under treatments was unexpected. Maple and Finlay (1986) reported that in enriched habitats, especially those that provide complex foraging opportunities, the levels of some affiliative interactions can decline. Glatson, *et al.* (1984) found that cotton-top tamarins that were placed on display exhibited less affiliative behavior, including allogrooming, compared to another group of cotton-top tamarins which were not in public view.

Moynihan (1970) and Dawson (1979) reported that allogrooming is most likely to occur in the early morning, before active foraging has begun. If this pattern was expressed by the subjects, then it is probable that a considerable amount of allogrooming data were not recorded, simply because data collection commenced later in the day. This might also occur with enrichment strategies that bring about increases in vigilance behaviors, e.g., scanning and scent marking. To the extent that an enrichment strategy increases vigilance behaviors, and, conceivably, levels of arousal, the rate of allogrooming might be expected to decline. Allogrooming also declines if other locomotor behaviors increase (Welker and Luhrmann, 1978).

The consistently higher rates of social grooming under conditions featuring the sounds of wild tamarins engaging in affiliative social interactions suggests that this type of acoustic treatment should be further investigated. It is conceivable that the provision of this type of acoustic treatment could serve to mask the unnatural acoustic habitats characteristic of zoos and laboratories.

The pronounced sexual dimorphism in the change in rates of allogrooming is difficult to explain, especially the reduction in the frequency with which the female groomed the male. In all Callitrichids, however, the frequency with which males groom females is strongly influenced by her reproductive condition, rising to a maximum during peak estrus, and, in some species, immediately preceding parturition (Woodcock, 1984; Epple, 1975; French, et al, 1984). During the course of this study, the animals exhibited copulatory behavior and produced young twice. The magnitude of this factor compared to the possible influence of the treatments on the behavior of the tamarins cannot be accurately assessed. In fact, although the reproductive state of the female could not be accurately determined during the study, the finding that the male consistently engaged in high rates of allogrooming suggests that the reproductive state of the female was influencing the expression of this behavior. However, because the assessment of the reproductive state of female Callitrichids is so difficult, it is only possible to speculate about its possible role in modulating the rate of allogrooming.

The rate of allogrooming is also apparently influenced by the actions of zoo visitors. Glatson, Geilvoet-Soeteman, Hora-Pecek, and van Hooff (1986) reported that tamarins respond to some aspects of the zoo environment by exhibiting reduced rates of affiliative behaviors. The trend was especially apparent when animals were placed on display in the presence of large groups of zoo visitors. Whether or not this same effect operated during the course of this study is difficult to ascertain, since most data were collected during visiting hours. However, unless the behavior of visitors was wholly inappropriate, the subjects tended not to exhibit overt responses to their presence. When they did respond to overt solicitations by the public, all social interactions ceased for some period of time.

The role that the acoustic habitats of captive animals play in modulating levels of arousal or in facilitating social interactions is still poorly understood. Certainly, excessively loud or arousing acoustic phenomena might reduce the frequency of affiliative behaviors. Conversely, the application of environmentally relevant sounds at appropriate sound pressure levels might provide a means of acoustically isolating animals from unnatural acoustic surroundings, possibly fostering increased rates of affiliative social interactions.

Autogrooming

When the baseline scores are compared to the combined treatment and intertreatment scores, autogrooming significantly increases with treatments ($\chi^2 = 9.28$, $\underline{n} = 912$, $\underline{df} = 1$, $\underline{p} < .01$).

The hypothesis tested with this measure states that the frequency of autogrooming should increase when the animals are exposed to the treatments, especially those that might slightly arouse the subjects, e.g., all treatments except treatment 3 (Tinbergen, 1952).

There is a pronounced sex difference in the response of the animals to the treatments. The male groomed himself more than twice as frequently as the female groomed herself.

During the baseline, the male groomed himself during 251 intervals, while the female groomed herself during 159 intervals. Under the 16 conditions, the male groomed himself during 344 intervals, while the female groomed herself during 219 intervals.

When individual conditions were considered, there were no clear trends in the rate of autogrooming. There was a slight trend for the rates of autogrooming to be higher during treatment intervals when compared to intertreatment intervals, but these comparisons yielded no significant results. There was a slight decrease in autogrooming as each observation day progressed, probably an artifact of the collection of fewer data during afternoons.

It has been proposed that autogrooming can function as a modulator of arousal (Tinbergen, 1952). In situations when animals experience conflicting motivational states, displacement activities are often observed.

In a study of *S. o. oedipus*, the frequency of autogrooming declined when the level of locomotor behaviors increased (Welker and Luhrmann, 1978). When animals are aroused, there can be a reduction in maintenance activities and an increase in vigilance behaviors. To the extent that autogrooming functions as a maintenance activity, and not as a displacement activity, the results are not unexpected. Conversely, to the extent that autogrooming serves as a modulator of arousal, then increased autogrooming suggests elevated levels of arousal.

Because of the conflicting models that have been proposed to explain the function of autogrooming, it is difficult to explain the observation that the rate of autogrooming increased under treatment conditions. To the extent that autogrooming increases along with other behaviors often correlated with elevated levels of arousal, e.g., scent marking, display behaviors, and scanning, the increase in autogrooming might indicate that the animals were slightly aroused and engaging in the regulation of stress through displacement activities. This suggests that the treatments were functioning as mild stressors to the subjects. However, the changes in the frequencies of some other measures does not support this contention. Scanning, for example, occurs at a relatively high basal rate in tamarins, increasing when animals engage in vigilance behaviors. While increased vigilance implies increased attentiveness to the surroundings, it does not necessarily imply elevated arousal levels (Caine, 1984). If it were a reliable measure of arousal, the changes in the frequency of scanning would not necessarily suggest elevated reactivity in the subjects. The same is true for the change in the rates of scent marking, which while indicative of increased territorial defense, are still relatively low. Perhaps the most parsimonious explanation for an increase in autogrooming was the simultaneous decrease in allogrooming. Under treatment conditions where the subjects engaged in fewer social interactions, including allogrooming, they simultaneously increased the levels of self directed behaviors, including autogrooming. Suffice it to say that modification of the acoustic surroundings of some captive animals might provide a method for altering the rates of some maintenance activities, including autogrooming. Care should be exercised to employ treatments which do not unnecessarily arouse the subjects, possibly inhibiting the performance of social interactions.

Foraging and Environmental Exploration

When the baseline scores are compared to the combined treatment and intertreatment scores, there was no significant change in the frequency of foraging ($\chi^2 = 1.76$, $\underline{n} = 1979$, $\underline{df} = 1$).

When the scores for conditions 7 and 7' are compared, foraging significantly increased with treatments ($\chi^2 = 6.53$, $\underline{n} =30$, $\underline{df} = 1$, $\underline{p} <.05$).

The hypothesis tested with this measure states that the frequency of foraging should decrease slightly when the animals are exposed to treatments. The rationale for expecting a slight reduction in the frequency of foraging was that the animals would interrupt their foraging to scan or to engage in other vigilance behaviors.

The results show a slight decrease in foraging activity, but the magnitude of the change is not significant. During the baseline, the male foraged during 493 intervals while the female foraged during 532 intervals. When the totals for all of the conditions were considered, the male foraged during 477 intervals while the female foraged during 464 intervals. Only when conditions 7 and 7' were compared was there a significant difference between a treatment condition and the following intertreatment interval. Under condition 7, the male foraged during 14 intervals, while the female foraged during 1 interval. Under condition 7', the male and female each foraged during 4 intervals ($\chi 2 = 6.53$, $P<.05$).

Condition 7 featured the sounds of several captive cotton-top tamarins emitting "C chirps," "squeals," "partial quiet long calls" and "long call choruses." This result is difficult to explain, as foraging was not predicted to increase in response to the vocalizations of other tamarins. One possible explanation for this finding involves the presence of "C chirps" in the complex of vocalizations in condition seven. "C chirps" are often emitted by tamarins in food related situations (Cleveland & Snowdon, 1982). It is conceivable that the presence of this call element was perceived as another animal which had procured some item of food, suggesting that food was available, hence the increase in foraging by the subjects.

While there were individual differences between the animals in the rate of foraging, they are not consistent, constantly reversing throughout the course of the study. During some conditions, the female was much less likely than the male to forage, but she was also less likely to be visible.

Several species of Callitrichids exhibit sex based differences in foraging and food related behaviors. For example, Tardiff, et al, (1981) has found that animals housed in isolation consume more food than those held in social groups, primarily due to increased food competition. When there are pairs of tamarins housed together, females usually obtain preferred food items before males. In common marmosets and cotton-top tamarins, when competition for food results in aggression, females usually prevail over males (Tardiff & Richter, 1981). Males housed singly consume more food than females or subadults of either sex, but when they are placed into social groups, they consume less than adult females. Consequently, it was not unexpected that the female should engage in more food related foraging than the male.

One potential problem encountered when considering these findings is that it is difficult to distinguish between exclusively food related foraging and exploratory behavior. While most exploratory behavior was food related, it was not exclusively so, that is, not all foraging involved consumptive behavior. Some foraging probably represents a type of maintenance activity. The finding that the treatments did not inhibit its expression implies that the particular suite of acoustic variables employed in this study did not elevate levels of arousal in the subjects or that they were particularly ineffective in modulating this behavior.

Enrichment strategies designed to modify the expression of foraging behavior are likely to be more effective if they involve changes in the spatial and temporal presentation of food. For example, competition for food can be reduced by dispersing it around the enclosure in several food dispensers (Maple & Finlay, 1986).

The number of intervals within which foraging occurred declined during afternoons, both because of reduced data collection, and because the subjects exhibited reduced foraging in the afternoon. Virtually all Callitrichids display a bimodal pattern of foraging, with relatively low frequencies immediately after the animals arise, an increase in the mid-morning, a mid-day reduction, and a final intense period in the mid-afternoon. The initially low frequency of foraging is associated with a state of torpor, assumed by all Callitrichids during the evening (Hershkovitz, 1977). The mid-morning foraging period usually involves the acquisition of insect prey, extending for periods of up to 3 hours in Geoffroy's tamarin (Dawson, 1979; Garber, 1984a; Yoneda, 1984b). The mid-day reduction in foraging is associated with increased rates of resting and grooming. Finally, during the middle of the afternoon, there is a resumption in foraging, with an emphasis on the acquisition of plant materials. Foraging declines rapidly in some species as animals prepare to return to their nest boxes (Caine, 1984). Neyman (1978) reported that foraging was highly correlated with scanning, a finding that was not confirmed during this study.

Occasionally, the animals were recorded as exploring or feeding when tongue flicking was observed. This behavior is associated with sexual encounters and with environmental exploration, especially of objects with potential food value, usually immediately preceding or following ingestion, and probably involves a chemical assessment via the vomeronasal organ.

The special abilities of each species should be featured by zoos as much as possible. The distribution of food within enclosures can be accomplished in ways that challenge animals to express species typical behaviors, in ecologically relevant pursuits. Glatson, Geilvoet-Soeteman, Hora-Pecek, and van Hooff(1986) reported that increased foraging opportunities provide a means of improving inadequate housing by facilitating increased environmental exploration. Animals will persist in task related activities in order to procure food, even in the presence of ad libitum food, suggesting that activities related to foraging might in themselves be reinforcing (Carder & Berkowitz, 1970). Captive tamarins, for example, can be provided with opportunities to forage, while simultaneously being provided with problem solving tasks. Saddleback tamarins have shown that they are capable of remembering the location and features of objects for up to 24 hours. Their problem solving abilities appear to be better when tested under naturalistic conditions compared to results obtained under traditional testing regimens, suggesting that a more accurate appraisal of the behavioral capabilities of a species can be acquired under ecologically relevant testing conditions (Menzel & Juno, 1985).

The foraging strategy of Callitrichids is unique among primates. It is adapted to most efficiently exploit the temporal and spatial distribution of preferred fruits (Izawa, 1978; Dawson, 1979; Terborgh, 1983). Because the fruits that are important in the diets of tamarins grow in small, incremental units and ripen in a sequential order, the animals are constantly foraging selectively for fruits that have attained the proper stage of ripeness. This can account for the constant, low level of foraging that is observed in most captive Callitrichids.

One problem encountered during this study was that a more random regimen of food deposition was adopted by the zoo staff during the middle of the study. In late 1986, caretakers began to distribute some items of food, including live crickets, randomly within the enclosure. This change in the feeding regimen probably influenced both the rate of foraging and possibly altered modal positional behavior as well. This provisioning probably encouraged a constant, low level of foraging. The introduction of live prey probably dampened the effectiveness of condition 3, the cicada chorus, on the behavior of the subjects.

Up to 11% of the daily time budget of Geoffroy's tamarin is spent foraging. To the extent that Geoffroy's tamarins and cotton-top tamarins are comparable, similar values can be assumed for cotton-top tamarins, though, because Geoffroy's tamarins are slightly more insectivorous, they could expend slightly less energy on foraging than cotton-top tamarins.

When live prey were introduced into the enclosure, the frequency of foraging was expected to increase. In free living Geoffroy's tamarins, up to 87% of all foraging involving locomotor behaviors including clinging and leaping is associated with insectivory, while 76% of more passive foraging is associated with the consumption of foods derived from plant material. Reasonably, the rate of locomotor activity could have been expected to increase with the introduction of live prey, though the data do not support this contention.

The effectiveness of acoustic treatments in influencing the expression of foraging behavior has not been demonstrated during this study. The rate of foraging and related behaviors is probably more susceptible to alteration through changes in the spatial and temporal disposition of food and by changes in the diameters of resting and climbing structures associated with food dispersal.

Not Visible

Although the absence of an animal does not constitute an observable behavior, it can be a result of experimental manipulation and is considered here as a dependent variable in order to obtain an exhaustive list of behavioral categories.

When the baseline scores are compared to the combined treatment and intertreatment scores, the animals were not visible significantly more often with treatments ($\chi 2 = 133.79$, $n=517$, $df=1$, $p<.001$).

While there was no specific hypothesis tested with this measure, there was a desire to observe the possible effects of acoustic treatments on cryptic behavior in these potentially reactive subjects. Any decrease in visibility might indicate that the animals were being stressed by the experimental procedures, something that should be considered whenever there is a change in the enclosures of animals that can not withdraw from aversive conditions. Results indicate that during treatments, the animals were significantly more difficult to observe. During the baseline, the male was not visible during 37 intervals while the female was not visible during 90 intervals. During the combined treatments, and intertreatment conditions, the male was not visible during 146 intervals while the female was not visible during 228 intervals.

The female was more than twice as likely as the male to evade detection. Under condition 4 and the following condition 4', the animals were both not visible during a relatively high number of intervals. Under condition 4 the male was not visible in 20 intervals while the female was not visible during 23 intervals. Under condition 4', the male was not visible during 17 intervals while the female was not visible during 27 intervals.

It is probable that the results obtained under this condition were spurious, no other dependent measures are well correlated with this treatment, a complex combination of calls from wild Geoffroy's tamarins engaging in relaxed social behavior. There is also no clear explanation for the greater number of intervals during which the female was not observed compared to the male. It was suggested by some observers that the female was sometimes returning to the nest box during the day, though this was difficult to confirm.

The subjects were extremely small and difficult to observe under certain lighting conditions. Further, the enclosure was heavily planted and provided many opportunities for the animals to conceal themselves, a desirable state of affairs in nature.

Disturbances outside of the enclosure might have influenced the amount of time that the animals were not visible. Wolters (1977) reported that disturbing external phenomena often caused captive cotton-top tamarins to retire to their nest boxes at times of the day unusual for this behavior.

Of particular interest is the finding that both animals were not visible under condition 4. Although there are insufficient data to support the suggestion that the animals were engaging in relaxed social behavior in a secluded portion of their enclosure, the possibility still exists. This particular treatment has been implicated elsewhere in facilitating social interaction, especially allogrooming.

The increased level of crypsis during treatments is potentially important. This trend continued even as the observers improved and were less likely to miss the subjects. The data seem to imply that, for some reason, the animals were avoiding the more open areas within the enclosure under the treatment conditions. Nonetheless, there were no other overt manifestations of stress or arousal in the subjects clearly associated with the treatment variables. Consequently, the finding that the animals were less likely to be visible under the treatments conditions cannot be attributed with certainty to the effects of the manipulations.

Cage Location

Garber (1984a) distinguishes between postural and positional behavior, each of which represents an extreme locus along a conceptual continuum of locomotor behavior. Position indicates "where" an animal is in an enclosure, while postural data describes "how" an animal is. The rationale for recording positional information was to attempt to detect any change in modal position over time that might have occurred under the influence of the treatments. There was no hypothetical model being tested, though originally there was an interest in determining whether or not animals could be coaxed into the upper portion of the enclosure, resulting in less time spent foraging on the substrate. Excessive contact with the substrate exposes animals to feces and moist soil, sometimes resulting in increased parasitic infections and fungal infections of the integument.

Throughout the baseline study, the animals preferred the upper rear quadrant of the enclosure. The male was located in the upper right rear quadrant most of the time (n = 104), while the female was located in the upper left rear quadrant most of the time (n = 78). The least occupied quadrant was the right, lower, front section of the enclosure, closest to the observers. The male occupied this quadrant during only one interval while the female was observed there in 14 intervals. This preference persisted throughout the entire study, not changing significantly from the baseline condition even after treatments were administered. The only notable finding was that the male and female seldom occupied the same quadrant simultaneously, except when allogrooming or mating.

The next most frequent locational configuration involved a reversal of the most frequently observed pattern, with the animals occupying the favored quadrant of the other animal.

These findings differ from those of Box and Morris (1980) who reported that mustache tamarins spent up to 46% of the time on the substrate of their enclosure.

Snowdon, et al (1985) reported that in a colony of *S. o. oedipus*, the animals spent most of their time at levels in the enclosures above one meter.

In an enclosure similar to the housing at the San Francisco Zoo, Larsson, Hagelin, and Hjern (1982) reported that the movement of pygmy marmosets within the enclosure was difficult to record accurately. This was a function of the complex vegetation that the enclosure featured and the rapid bursts of locomotor activity characteristic of Callitrichids. Similarly, when the tamarins began to move about in their enclosure, the activity was difficult to record accurately. Consequently, the results presented here are more reliable for describing state events and for assigning modal positions than for inferring changes in locomotor activity.

Glatson, Geilvoet-Soeteman, Hora-Pecek, and van Hooff (1986) reported that in some zoo habitats, compared to quieter laboratory settings, cotton-top tamarins show less affiliative behavior. This could partially explain why the animals spent so little time in the same quadrant.

An insignificant change in the location scores does not necessarily imply an absence of locomotor behavior. Again, positional and postural behaviors must be distinguished from one another (Garber, 1984). The location of the animals was often closely associated with specific activity patterns. For example, foraging was usually performed on supports having diameters of 10 cm or less. These were available at several locations within the enclosure. Feeding, however, usually was performed on supports with diameters exceeding 10 cm, including shelves.

Locational scores were somewhat affected by the presence of heat lamps, which often attracted the tamarins, probably obscuring any influence that the acoustic treatments might have exerted on locational behavior.

Suffice it to say that there was apparently no significant change in modal locational behavior throughout the course of the study.

General Findings

The finding that overall vocalizations increased was precisely what was predicted. The concurrent finding that the individual rates of vocalization were lower than expected was an artifact of the inability of the observers to accurately identify the vocalizing animal. Surprisingly, the animals did not respond in kind to the "long calls" of *S. o. oedipus* as suggested by the findings of Cleveland and Snowdon (1982). This was less surprising when responses to treatments featuring the vocalizations of *S. o. geoffroyi* were considered. Whether the magnitude of the responses was unusually low is not clear. Vocalizations should have increased under all treatment conditions except, possibly, condition 3, a recording of a cicada chorus.

The finding that allogrooming declined under all but one condition was unexpected. It is possible that the animals engaged in fewer bouts of allogrooming because they were exhibiting increased rates of autogrooming or were engaging in greater frequencies of crypsis. In fact, some of the lower values observed for several measures could be partially explained by the increased probability that an animal was not visible. For example, scent marking, especially by the female, was predicted to increase in response to treatments 1, 5, and 7, all of which feature elements of conspecific intertroop vocalizations. The finding that this did not occur suggests that some scent marking could have occurred on the substrate, where the animals were not visible to observers. Even when the animals were visible, scent marking often consisted of any one of several related behaviors, many of which were subtle and easily missed by observers.

The finding that scanning declined was also unexpected. In agreement with Welker and Lurhmann (1978) the male scanned more than the female. This is probably a function of the greater role that the male plays in territorial monitoring. However, the rate of scanning was expected to increase in response to all variables. The only comparison which yielded a significant increase in scanning was that between condition 3, a cicada chorus, and 3', the following intertreatment interval. This finding suggests that the animals were attempting to locate potential items of prey.

If, as proposed by Welker and Lurhmann, scanning is important in territorial defense, then an increase in scanning should have been correlated with an increase in other measures indicating higher levels of arousal, including scent marking, display behaviors, and possibly autogrooming. What was observed was a decline in scent marking and scanning, implying that the overall level of arousal was probably not influenced under the treatment conditions.

This finding does not explain the decline in allogrooming and the simultaneous increase in autogrooming. In fact, compared to the baseline, the overall level of activity appears to have declined under the treatments.

This contradicts one of the original goals of this study, which included a desire to investigate the possibility of employing acoustic phenomena to modulate the overall level of locomotor activity, especially in species that can exhibit reduced levels of activity in impoverished settings.

One of the most interesting findings was that under all 4 conditions featuring the vocalizations of free living tamarins engaging in social behavior, allogrooming consistently increased. These acoustic variables often featured affiliative vocalizations and might have functioned as non-threatening acoustic maskers of other acoustic phenomena for the subjects.

The finding that display behaviors were not frequently observed and that they actually declined under the treatment conditions was unexpected and tends to suggest that the cross modal effectiveness of the treatments on altering rates of behavior was minimal. If true, this would imply that the most effective means of influencing vocal behavior is through the application of acoustic treatments. Additionally, visual scanning, foraging, and scent marking behavior would be more effectively modulated by introducing visual stimuli, items of food, and olfactory stimuli respectively.

The finding that the rate of foraging was not influenced by the treatments was not surprising. To the extent that animals engage in vigilance behaviors or startle responses under treatment conditions, the rate of foraging could have been expected to decline. To the extent that affiliative behavior, including cooperative foraging, was fostered by the treatment conditions, the rate of foraging could have been expected to increase. The actual scores for foraging, as with those for other measures, were strongly influenced by the number of intervals during which animals were not visible. Animals were significantly more likely not to be observed under treatment conditions than during the baseline. It is possible that, following the presentation of potentially arousing treatments, the animals became inactive and engaged in increased cryptic behavior.

Of greatest concern to managers of potentially reactive endangered species is the influence of stressful stimuli on feeding and reproductive behavior. If animals are highly aroused, for example by experimental treatments, the amount of time spent in vigilance activities could detract from the expression of affiliative and social behavior. If the increased levels of arousal result in increased agonism within groups, then the procedure is undesirable. Conversely, if the performance of territorial behavior, including displaying and scent marking, serves to enhance social and sexual interactions, then the experimental or management procedure is desirable.

With regard to this study, there are simply too few data available on which to base strong conclusions. Minimally it can be stated that there were no obvious negative influences on foraging, feeding, or sexual behavior.

Under all but one condition, there was no significant change in the frequency of foraging. This finding suggests that the treatments exerted little influence on maintenance activities.

With regard to the probable change in levels of arousal under the treatment conditions, the data are ambiguous. Scanning, for example, showed a decline, suggesting that the animals were not engaging in increased territorial monitoring. This implies that the treatments featuring vocalizations of other tamarins were not perceived as indicating the presence of potential competitors, though the subjects simultaneously exhibited an increase in autogrooming, possibly an indicator of elevated arousal. Obviously, more research on the functions of scanning and grooming needs to be conducted to resolve this confusing finding.

Since the study apparently exerted no negative influences on the subjects, and since it provided a forum for informing the public about the conservation status and complex vocal behavior of tamarins, this type of enrichment strategy should be encouraged. Some suggestions for future researchers are provided here.

Playback studies involving primates are notoriously difficult (Byrne, 1982). Trials must be relatively infrequent to reduce habituation effects, yet many trials are necessary to obtain sufficient data. These conflicting requirements are difficult to balance. The possibility of overstimulating captive animals exists, and can disrupt the behavioral equilibrium of an animal (van Hooff, 1986).

Shortcomings in materials, methods, and design sometimes do not become apparent until a study is well under way. Among the most important shortcomings of this research was the singular absence of control over the subjects and testing situation. Conceivably, some of the reasons for the low amplitudes of response included the influence of extraneous factors, including the early histories of the subjects, distracting external visual and acoustic phenomena, insensitive sampling procedures, and imperfections in the acoustic treatments (Lehner, 1979). In research involving the introduction of acoustic treatments to primates, loudspeakers must be hidden from the subjects or they will often cease to respond (Byrne, 1982). Morton (1975) reported that as the distance between a loudspeaker and a subject decreases, the ratio of direct to reflected sound increases, possibly reducing the apparent authenticity of the treatments to the subjects.

Many primates require the presence of a visual referent in order to exhibit responsiveness to acoustic phenomena (Redican, 1975; Masataka, 1983a), though Moynihan (1969) suggests that this is less true in Callitrichids, primarily because of the arboreal nature of their habitats, which can impede visual signals.

To the extent that the treatment variables differ from authentic aspects of an organism's habitat, their validity and effectiveness will be reduced. For example, Dablesteen (1981) has emphasized the importance of appropriate sound pressure levels in the design of sound playback studies. Excessive sound pressure levels can result in animals rapidly habituating to the stimulus, responding aggressively, or attempting to avoid the stimulus. The amplitude of a vocalization is often a modulable parameter of a signal. The sound pressure levels employed during this study were commensurate with those employed in similar research (Epple, 1968; Masataka, 1983a; Cheyney & Seyfarth, 1985).

Because 7 of the treatment conditions featured the calls of either conspecifics or congeners, elevated rates of territorial defense behaviors, including scanning, scent marking, and vocalizations were expected (Cleveland & Snowdon, 1982). The expected influence of the treatments on the rates of allogrooming and autogrooming was not observed, but it was reasonable to expect these measures to show a decline in frequency if the subjects were otherwise engaged in vigilance behaviors. The expected influence of the treatments on reproductive behavior was unclear at the onset of the study, though ultimately the effect appeared to be slightly negative. Obviously there are too few data to support conclusions regarding this finding, though Gamble (1982) reported that excessively intense or chronic sound could inhibit reproduction in some laboratory animals.

The inadvertent use of the vocalizations of *S. o. geoffroyi*, in addition to those of *S. o. oedipus* probably reduced the effectiveness of the study. While there are similarities in the vocal morphologies of all Callitrichids, especially with calls serving similar functions (Epple, 1968), the calls of the two subspecies of *Saguinus oedipus* are subjectively different. The calls of *S. o. geoffroyi* appear to have higher fundamental frequencies and seem to be extremely variable compared to those of the captive *S. o. oedipus*. These treatments were chosen at a time when the taxonomic status of these two tamarins was unclear. Some researchers, especially those working with Panamanian tamarins, often failed to distinguish between the two animals in their research.

One advantage to the use of the recordings of wild tamarin vocalizations was that these recordings featured some acoustic elements from natural tamarin habitats. The recordings from the Wisconsin Regional Primate Center were often marred by metallic cage noise. Consequently, it was difficult to maintain that one set of treatments was necessarily more valid than the other.

The use of fixed interval presentations for the treatments poses problems, including a tendency to habituate subjects to the treatments. Some research indicates that these effects might be age dependent. In a study of recovery from habituation to the fixed interval presentation of novel objects, Harrison and Isaac (1984) discovered that the addition of auditory stimuli disrupted recovery in older squirrel monkeys more than in younger monkeys. Older animals were more highly aroused by irrelevant, novel stimuli than young animals. Younger animals, while initially aroused when confronted with irrelevant, novel stimuli recovered from this reaction and exhibited a less pronounced reaction to stimuli. In other words, when irrelevant, novel auditory stimuli were presented to young monkeys, they were less susceptible to habituation. Another implication of this research is that younger animals are less likely to show inhibition of behavior when confronted with auditory stimuli. In older squirrel monkeys, auditory stimuli resulted in a dampening of the scalloping in the temporal patterning in frequencies of behavior. This research suggests that acoustic enrichment schemes, or for that matter, other enrichment procedures featuring fixed interval presentations are more effective in younger animals, as were the subjects in the current research. The use of acoustic enrichment schemes with older animals might lead to a reduction in certain types of behavior. Older animals seem to exhibit a decline in their ability to ignore irrelevant acoustic stimuli, impairing performance on other tasks, while younger animals seem to habituate quickly to irrelevant acoustic stimuli and can more quickly resume earlier schedules of behavior (Harrison & Isaac, 1984). Herzog and Hopf (1984) employed a fixed interval presentation of alarm calls to isolate-reared squirrel monkey infants and found that the animals habituated rapidly to acoustic stimuli, though the rate of habituation was reduced when a visual stimulus was presented along with the acoustic stimuli.

Acoustic enrichment could be an important means of facilitating learning in captive primates. Learning is encouraged by animals watching other animals direct their attention toward the appropriate object, including sound sources (Masataka, 1983a). The opportunity to orient toward and to track relevant acoustic stimuli could improve sensory and motor development in young animals (Knudsen, 1984). These procedures could be important in encouraging animals to learn to recognize important acoustic aspects of their natural surroundings, possibly critical for animals targeted to be rereleased into the wild.

The selection of the most effective acoustic treatments is often difficult. Selection of treatment variables assumes that some concept of the function of a particular vocalization is already known, unless this is the basis of the proposed research. Studies involving the relative responsiveness of various Callitrichids to the vocalizations of congeners would be valuable, especially if this research assisted in the resolution of taxonomic questions. This could become an important consideration as the space available in zoos and laboratories for the maintenance of sub-specific forms of endangered species becomes increasingly valuable.

The choice of response measures is as fraught with difficulty as is the choice of playback treatments. For example, there were several locomotor patterns that the subjects regularly exhibited, and which have been reported to occur in the wild, for which no categories were provided on the sampling instruments. There are bouts of extremely active horizontal running intermingled with jumping, leaping, and rough and tumble play, often expressed in diurnally bi-modal peaks of activity (Neyman, 1978; Welker & Luhrmann, 1978). The subjects exhibited peaks in these activities near 10:30 and again at 14:30 on a regular basis. In the wild, as well as in this study, during quiet periods the animals often engaged in allogrooming. Neyman (1978) reported that wild cotton-top tamarins usually exhibited a mid-day lull in activity, something that was also observed during this study, yet something that the sampling instrument made it difficult to record. Usually, there was a quiet period during the late morning at about 11:00 and again in the early afternoon at about 14:00.

In the wild, tamarins become more quiescent in the late afternoon, usually around 16:30, nearly the same time at which the study subjects exhibited quiescence. During these quiet periods, there were few vocalizations in either the wild troops or in the study animals. These strong diurnal patternings in levels of behavior probably masked the influence of the treatments.

It is worth noting that the subjects appeared to maintain the same diurnal cyclicity as wild conspecifics. This is interesting because of the latitudinal displacement of the subjects, which has been implicated in the temporal shifting in the patternings of behavior in translocated neotropical animals (Erkert, 1986). In fact, in common marmosets, temporal patterning can be buffered with the application of acoustic treatments, especially sounds of nearby conspecifics, possibly accounting for a slight attenuation in the expression of some behaviors. Reduction in the frequencies of some behaviors could indicate an increase in cryptic behavior.

There were several environmental factors beyond the control of the researchers which could have influenced the subjects, including relative humidity, temperature, and photoperiod. Dawson (1979) found that in Geoffroy's tamarins, the amount of time spent foraging was reduced by a third on extremely humid or rainy days. The absence of a functional environmental control system often resulted in extremely high levels of moisture within the enclosure, frequently exceeding 80% relative humidity, possibly attenuating the rates of some behaviors.

The mean temperature within the enclosure was slightly lower than the typical temperatures reported to be in much of the literature on neotropical fauna. Temperature and humidity could not be continuously monitored, and their unnatural levels and concomitant influence on the subjects was unclear.

During the winter months, heat lamps within the enclosure were illuminated for 24 hour periods to maintain internal temperature. The lengthened photoperiod could have exerted some influence on the diurnal cyclicity in the patterning of behavior of the subjects and could have affected the reproductive cyclicity of the female. The presence of illuminated heat lamps influenced the positional behavior of the animals as well, especially the male, who often entwined himself around them in cold weather.

During the course of the study, both observers and zoo visitors had difficulty locating the tamarins. In order to allow the public to better observe the animals, much of the vegetation in the enclosure was removed during the study. This procedure severely confounded the 'not visible' category, making the animals slightly easier to locate, and influenced the modal locations of the subjects, by reducing their tendency to be found on the west wall of the enclosure.

Appropriate species for the study of responsiveness to changes in their acoustic surroundings include those that exhibit complex vocal behavior, as do cotton-top tamarins. Menzel and Juno (1985) have described tamarins as highly alert, visually curious, and reactive, responding to any source of change in their surroundings. Unfortunately, they also habituate rapidly to many types of stimuli and show little or no spontaneous recovery from treatments. Again, this characteristic could have influenced the results of this research.

Its shortcomings notwithstanding, this type of research can simultaneously investigate the influence of captivity on behavior, suggest ways of improving captive environments, and provide basic information about the behavior of endangered species. The use of the zoological park as a locale for research provides those who advocate the continuance of these institutions with a valid reason to continue supporting them. Zoological parks should increasingly emphasize research on the biology and behavior of their exotic fauna. Information gathered from these studies should then enable the design of habitats to be improved, both for the animals housed within them and for the improved education of the zoo visitor. To the extent that zoos improve the lives of their animals, improve the quality of their educational programs, and improve their ability to support research, they will secure a position for themselves in the world of the future.

For too long, zoos have displayed animals in an inappropriate vacuum. Indeed, some have termed zoos "living museums". Unfortunately, while exhibiting living organisms, many zoos have failed to exhibit behavior. In order to facilitate its expression in captivity, habitats need to provide animals with ecologically relevant behavioral opportunities.

This study was an inaugural attempt to address the influence of the acoustic habitat on the behavior of captive tamarins.

Though some results are inconclusive, others are promising and suggest that there should be more research in this area.

CONCLUSIONS

The role of the contemporary zoological garden is changing from one that emphasized entertainment and recreation to one that emphasizes education and research.

Studies that bring together representatives of the scientific, academic, and animal care communities offer a unique opportunity for the sharing of information and the resolution of management problems, while training a new generation of behavioral scientists.

Environmental enrichment schemes have frequently emphasized the modification of the visual aspect of habitats by improving the appearance of an animal's enclosure. There has been little emphasis on the investigation of the influence of acoustic surroundings of captive animals on their behavior.

This research has attempted to explore the use of acoustic phenomena to encourage natural behavior in captive cotton-top tamarins.

In response to the sounds of laboratory reared conspecifics, free living congeners, and common prey, the subjects exhibited significant increases in the rates of vocalization, autogrooming, and cryptic behavior, while exhibiting significant decreases in the rates of scanning, allogrooming, displaying, and sexual behavior. The rate of scent marking, foraging, and the modal location did not significantly change.

Some of these results are contrary to the findings of other researchers. The research seemed to incite interest in zoo visitors and volunteers, many of whom became involved in the study. The study facilitated the cooperation of scientists, academics, and the zoo staff.

This research suggests that there should be a greater effort to utilize the unique resources of the contemporary zoological garden for behavioral and biological research. Zoos are particularly well suited for intensive studies investigating long-term changes in the behavior of individual animals, as opposed to studies emphasizing average differences in the behavior of large numbers of subjects.

To the degree that the animals housed in zoos encourage the concern of the public about critical conservation issues, they might be instrumental in forestalling the wholesale reduction in the biological diversity of the planet. The effectiveness of animals in evoking respect from the public is enhanced by displaying them in naturalistic surroundings that encourage the expression of natural behaviors.

Zoos are living museums and should emphasize the living over the museum. If zoos are successful purveyors of the conservation message, then the resulting preservation of biodiversity will insure that all of us will inhabit a truly enriched environment.

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Appendix A

Sampling Instrument

Appendix B

Digital Sonograms of Playback Variables

Sonograms were produced with a Kay Elemetrics Sound Analyzer (Models 5500 and 7800), which produced type B-65 sonograms. The display setting used was 3D, with the bandwidth set at 0 Hz to 8 kHz, frequency markers set at 500 Hz, analysis bandwidth filter set at 45 Hz, clip filter set to flat-top, mark level (grey scale) set to seven, and the dynamic range set to normal. Each centimeter represents 0.08 seconds horizontally. Total sample time is 2.54 seconds.

PV. One

This sonogram shows a call consisting of three primary segments. The first segment shows a fundamental frequency of 3.5 kHz, with a duration of 0.24 seconds. At 0.04 seconds, there is a dip to 3.0 kHz that continues through the first call segment. There is one harmonic, shorter in duration (0.18 seconds) at 7.1 kHz, descending to 6.5 kHz. The second segment of the call starts at 0.16 seconds, lasting for 0.08 seconds. The predominant frequency is 2.8 kHz, featuring no harmonics. The third segment of the call possesses elements similar to the first two segments. These are "F" chirps and "F" chirp trills, produced by captive *Saguinus oedipus oedipus* at the University of Wisconsin. These calls are important in intertroop communication.

PV. Two

This sonogram shows a complex combination of calls, beginning with a short (0.24 second) call element, followed by a 0.64 second interval. This short element possesses an inverted "J" configuration and an initial frequency of 6.4 kHz, with the predominant frequency at 4.5 kHz. There is some energy appearing at 6.5 kHz. There is some noise in the range of 3.5 kHz which appears at 0.99 seconds along the horizontal axis. The second call segment has a duration of 0.68 seconds. Its highest frequency is 7.25 kHz and its lowest is 3.25 kHz. The greatest energy is concentrated between 3.6 kHz and 6.0 kHz. The third call segment starts at 1.28 seconds and has a duration of 0.054 seconds. The predominant energy distribution is between 3.4 kHz and 6.1 kHz. At 1.42 seconds there is a rise in frequency from 4.0 kHz to 4.9 kHz which then falls rapidly to 3.5 kHz. Each of several "J" elements shows a start frequency of 4.0 kHz, a rapid rise to 4.9 kHz, and a terminal decline to 3.5 kHz. At 1.7 seconds there is a small call element with most of its energy concentrated at 3.5 kHz, rising to 4.0 kHz, descending to 3.5 kHz, and featuring a total duration of 0.056 seconds. This segment resembles the first call element but there is less energy in the terminal element. Many artifacts on the sonogram were produced by extraneous environmental noise. These vocalizations are those of wild *Saguinus oedipus geoffroyi*, recorded in Poco, Panama. Although from a distinct sub-species, they possess elements similar to "A" chirps, "b" chirps, "c" chirps, "g" chirps, "h" chirps, "b" trills, and small, initially modulated whistles described for *Saguinus oedipus oedipus*. The variability of these calls implies that they might possess several functions, including mobbing.

PV. Three

This sonogram shows four pulses of insect stridulation produced by cicadas, with the frequencies ranging from 3.0 kHz to 7.5 kHz. Each pulse is 0.48 seconds in duration.

PV. Four

This sonogram shows a complex of call elements with frequencies ranging from 3.5 kHz to 7.0 kHz. At 1.28 seconds, there is an element that is 0.4 seconds in duration. At 1.86 seconds there is a vertical band of energy. Adjacent to this band, at 1.94 seconds, there are smaller call elements. These calls are those of wild *Saguinus oedipus geoffroyi* recorded in Panama. Although not structurally equivalent to any distinct calls of *Saguinus oedipus oedipus*, these vocalizations subjectively sound "trill" like, as suggested by their high degree of frequency modulation. The terminal element resembles a compressed "A" chirp described for captive *Saguinus oedipus oedipus*, suggesting that this vocalization functions in mobbing situations. The remainder of the call is similar to the "b"trill, twitters, and multilevel whistles of *Saguinus oedipus oedipus*, complicating the attribution of a discrete unitary function to this vocalization.

PV. Five

This sonogram shows a call featuring three primary segments. The first element features a "J" configuration, with a frequency range of 3.0 kHz to 3.7 kHz. There is a detectable harmonic at 7.5 kHz. The second element features a frequency range similar to that of the first, ranging from 3.2 kHz to 3.7 kHz, with its maximum energy at 3.5 kHz. There is a noticeable harmonic at 7.5 kHz. There is a 0.12 second interval after which there is a diagonal element which descends from 4.5 kHz to 3.0 kHz, featuring a duration of 0.08 seconds. The terminal segment of the third element shows an increase in energy between 2.5 kHz and 2.7 kHz for approximately 0.32 seconds. These vocalizations consist of "F" chirps, partial quiet long calls, and long call choruses recorded from a breeding colony of captive *Saguinus oedipus oedipus* housed at the University of Wisconsin.

PV. Six

This sonogram shows a complex of calls with an initial element featuring a duration of 0.64 seconds and a predominant frequency of 6.75 kHz. At 0.10 seconds, the frequency falls to 4.25 kHz. This pattern is repeated several times during the sampling interval. The fundamental frequency is 3.8 kHz, with no measurable harmonics. There is a band of energy between 5.0 kHz and 6.0 kHz throughout the sonogram, possibly an artifact of extraneous noise. This call complex shows 25 separate elements with an interval of 0.08 seconds between each element. This call was recorded in Panama from a single *free living Saguinus oedipus geoffroyi* and sounds subjectively "trill" or "twitter" like, but possesses elements that structurally resemble the "B" trills and "C" trills of *Saguinus oedipus oedipus*, often heard in adult interactions with infants.

PV. Seven

This sonogram shows a complex of calls that include "long call choruses", "C" chirps, partial quiet long calls, and squeals from a large number of captive *Saguinus oedipus oedipus* housed in a breeding colony at the University of Wisconsin. The number of animals vocalizing simultaneously complicates the analysis of this spectrogram difficult. The predominant calls displayed are often emitted by animals engaging in inter-group and intra-group spatial regulation.

PV. Eight

This sonogram shows a complex of calls featuring five distinct segments. The initial call element starts at 0.44 seconds, the second at 0.92 seconds, the third at 1.40 seconds, the fourth at 2.21 seconds, and the fifth at 2.34 seconds. The initial segment displays an extremely low amplitude. The second segment features a range of frequencies between 5.0 kHz and 5.2 kHz. The third segment is the most complex element, starting at 3.5 kHz and rising to 6.5 kHz. The fourth segment features a frequency range between 5.0 kHz and 5.6 kHz. All five elements show the greatest energy in the range between 5.0 kHz and 5.5 kHz. The spectrogram features artifacts from extraneous environmental noise. This call complex was recorded in Panama from a single free living *Saguinus oedipus geoffroyi*. The elements exhibit structural similarities to "A" chirps, "multi-level whistles", and "B" trills of *Saguinus oedipus oedipus*. Again,the complexity of this call complicates the analysis of this spectrogram.

Appendix C

Hansen Frequency Tables

The following table provides total modified frequencies for all dependent measures.

Appendix D

Subject Responses by Treatment Conditions

Appendix E

Behavior Totals Over Baseline

Appendix F

Frequencies of Observed Locations

Appendix G

Responses With Location Across All Treatment Conditions

END