Gorilla Adaptations to Naturalistic Environments

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In the past few decades there have been increased investigations into the effects of captive environments on behavior. Simultaneously, zoological gardens have undergone a revolution in philosophy and design, resulting in a proliferation of “naturalistic” habitats. Complex environments such as these have been found to affect the behavior of captive animals favorably, including increasing reproductive and rearing success, encouraging the expression of species-typical behavior patterns, and decreasing abnormal behaviors.

In June 1988, Zoo Atlanta completed four naturalistic habitats for western lowland gorillas (Gorilla gorilla gorilla). These new habitats afforded a unique opportunity to study the adaptation of lowland gorillas to novel, naturalistic habitats. During the first year of habitation, a total of 451 hours of data were collected on 11 gorillas housed in three harem groups. Focal animal sampling with a behavioral change scoring system was used to obtain information on behavior, substrate, environmental components utilized, and location in sun or shade. Instantaneous scans at 15 minute intervals provided information on location and behavior of all individuals. Adaptation to the environments was assessed by using the indices of: time spent manipulating objects across the course of the study, the percent of the habitats utilized, and the dispersal of individual animals over the habitats. Trends in these behaviors indicated that exploration of the environments significantly decreased, but that this decline in exploration took over six months to occur. Several interpretations of these findings are presented including the unfamiliarity of these naturalistic habitats to these subjects.

Key words: western lowland gorillas, Gorilla g. gorilla, novelty, neophobia, naturalistic enclosures, enclosure utilization

INTRODUCTION

During the past several decades, scientists have become increasingly interested in evaluations of the effects of captivity on behavior. The effects on behavior of deprived environments, such as those described by Harlow and his students [e.g., Harlow and Harlow, 1962], are well-known. These effects include reductions in the
exhibition of species-typical behaviors and accompanying increases in the exhibition of stereotypic/abnormal behaviors [e.g., Erwin and Deni, 1979].

At least three reasons can be listed for identifying methods to improve the quality of captive environments: First, the new USDA regulations regarding psychological well-being in captive primates encourage us to learn more about providing adequate environments for these species [Animal Welfare Act Amendments, 1985]. Second, a factor of relevance primarily for zoological gardens is that exhibit animals should behave and be housed in ways that will most effectively educate zoo visitors [Finlay et al., 1988]. And last, of critical importance is increasing the expression of those behaviors associated with successful breeding and parenting. Beck and Power [1989] concluded that the majority of reproductive failures in captive gorillas are due to deficits in sexual behavior rather than to physiological factors.

Deficiencies in the social environment have been clearly linked to subsequent inadequacies in sexual behavior and parental care. In particular, the presence of both the mother and conspecifics during rearing positively affects the probability of future reproductive success [e.g., Harlow and Harlow, 1962; Beck and Power, 1989]. Physical variables of captive environments have also been shown to affect behavior, most notably reproductive behavior. Complex exhibits, which include most naturalistic exhibits, have been found to be related to positive behavioral outcomes in great apes. Miller-Schroeder and Paterson [1989] conducted a survey of successful reproduction and parental behavior in lowland gorillas and related environmental variables. A discriminant analysis revealed that several aspects of complex physical environments (e.g., visual cover, provision of natural vegetation) were related to appropriate breeding behavior and to successful parenting. Complex exhibits are also associated with alteration in activity to levels typical for the species [Wilson, 1982], reduction in stereotypic or abnormal behaviors [Akers and Schildkraut, 1985; Clarke et al., 1982; Erwin and Deni, 1979; Goerke et al., 1987; Gould and Bres, 1986; Pfeiffer and Koebner, 1978], and encouragement of species-typical levels of aggressive and affiliative behaviors [Maple and Stine, 1982; but cf. Clarke et al., 1982; Goerke et al., 1987]. Additionally, animals have been found to prefer complex, naturalistic exhibits over sterile alternatives when enclosure size is held constant [Timson, 1978; cited in Shettel-Neuber, 1988]. A current proliferation of naturalistic habitats in zoos across the world encourages us to further investigate the specific effects of such complex habitats.

In the summer of 1988, Zoo Atlanta completed construction of four new naturalistic habitats for lowland gorillas (Gorilla gorilla gorilla). The gorilla habitats are part of an African rain forest complex which also features an African aviary, with plans for future exhibits of mandrills, drills, guenons, and mangabeys. A post-occupancy evaluation of the completed design [Maple and Finlay, 1986, 1987; Zimmerman and Reizenstein, 1980] is being conducted to assess the effectiveness of the new exhibit by the perspective of all the facility users: staff, visitors, and gorillas. The results of this evaluation, including an examination of enclosure utilization by the gorillas and those environmental variables most relevant to differential usage of the enclosures, is currently in preparation (Ogden and Maple, in prep). The current paper will focus on the study of the gorillas and their adaptation to the new habitats, including an assessment of their response to the novelty these habitats represented and their exploration of these habitats.
TABLE 1. Subject listing

| Group        | Name  | Sex | Age* | Birth type/rearing |
|--------------|-------|-----|------|-------------------|
| Habitat I    | Rann  | M   | 26*  | Wild              |
| (Group 1)    | Choomba | F   | 26*  | Wild              |
|              | Shamba | F   | 30*  | Wild              |
| Habitat III  | Ozoum | M   | 28*  | Wild              |
| (Group 2)    | Paki  | F   | 26*  | Wild              |
|              | Machi | F   | 13   | Captive/mother    |
|              | Kuchi | F   | 4    | Captive/mother    |
| Habitat IV   | Calabar | M | 25*  | Wild              |
| (Group 3)    | Oko   | F   | 26*  | Wild              |
|              | Banga | F   | 20*  | Wild              |
|              | Radi  | M   | 6    | Captive/nursery with chimp |

*Asterisk indicates estimated age.

MATERIALS AND METHODS

Subjects

Subjects were 11 captive lowland gorillas (Gorilla g. gorilla) (see Table 1). These animals were housed in three harem groups, consisting of one silverback male, females, and juveniles. These animals are on long-term breeding loan from the Yerkes Regional Primate Research Center of Emory University. All have previously had limited outdoor access; however, only the gorillas in Group 1 (housed in Habitat I, see Fig. 1) have been housed for any significant length of time in large outdoor enclosures. In March 1989, two infants were born into Group 2 (housed in Habitat III). The animals housed in Habitat II are not included in this report as they were involved in a program of socialization during a portion of the study.

Animal Care

Feeding protocol. The animals are fed two main meals daily, consisting of fruits, vegetables, and monkey chow, with morning food scattered in the outside enclosure and evening food provided indoors. Browse and bamboo are scattered in outdoor enclosures daily, and cut fruit and vegetables are provided at least once daily to each group, generally in early afternoon.

Housing. Figure 1 presents a schematic illustration of the outdoor exhibits. Each of the four outdoor habitats is separated by double dry moats. Habitat I (housing Group 1) has approximately 2,100 square m (22,600 sq ft) of usable area (the remainder of the 2,700 square m habitat is excluded from the animals by electric fencing); Habitat II is 300 square m (housing the animals not included in the study); Habitats III and IV are 1,500 (16,100 sq ft) and 1,400 square m (15,000 sq ft) respectively (housing Groups 2 and 3). Each enclosure includes grass substrate, varied topography providing visual cover, rock outcroppings, large hardwood shade trees, saplings, bushes, and tree fells (see Fig. 2). Habitats 1 and 4 include waterfalls. The animals are housed in these outdoor exhibits from approximately 1000 through 1700 hours. During the remaining hours they are housed in indoor holding quarters, where they continue to be housed in family groups.

Procedures

Observations were conducted during the first year each group occupied its exhibit. Data for Groups 1 and 2 were collected between June 19, 1988, and June 18, 1989.
Fig. 1. Schematic illustration of gorilla habitats. Zoo Atlanta.
1989. Data for Group 3 were collected between August 13, 1988, and August 12, 1989. Observations were balanced across the hours the animals were on exhibit, seven days per week. Independence of samples was attained by maintaining an interval of at least one hour between observations on a given group.

A continuous behavioral change sampling method [Altmann, 1974; Crockett, in press] was used to obtain information on behavior, substrate, environmental variables utilized, and location in sun or shade. Within each group, focal animals were observed for 15 minute periods, the order of which was randomly selected for each observation period. A total of 451 hours of focal observations was completed on the 11 subjects, or approximately 41 hours of data per animal. Each hour of focal data consisted of four data points. Additionally, instantaneous scans at 15 minute intervals provided information on location and behavior of all individuals [Altmann, 1974; Crockett, in press]. Between 560 and 660 scan data points were obtained for each individual. The behaviors examined included those reflecting general activity patterns and those involving interaction with the environment, including object manipulation.

Dependent measures for the current analysis of adaptation to the habitats typify those used to study exploration or response to novelty. Exploration appears not to be a uni-dimensional behavior [Renner, 1987], including possible dimensions of specific and "diversive" exploration [Birke and Archer, 1983]. For this study, object manipulation was examined as a specific form of exploration, and measures of diversive exploration included the total percentage of the exhibits entered and an assessment of dispersal over the habitats vs. development of habitual usage. Object manipulation
was defined as the handling of available objects with hands, feet, or mouth, excluding the passive holding of objects.

Pairwise reliability coefficients were determined for multiple observers using unpreviewed videotaped sequences of behavior. Reliabilities for all observers averaged over 85%, using Cohen's Kappa statistic to account for chance agreement [Lehner, 1979].

Analysis

Data points for the analysis of object manipulation were the number of seconds per 15 minute focal sample spent manipulating objects. These durations were then plotted across the days of the study to investigate changes in this behavior over time. The data met the assumptions of homoscedasticity (Scheffe test of homogeneity of variance: 2.03, df = 7,141, P > .05) and uncorrelated error terms (Durbin-Watson statistic = 1.762, n = 141), allowing the use of a bivariate regression analysis to investigate trends in this behavior [Affifi and Clark, 1984; Neter and Wasserman, 1974].

A Kolmogorov-Smirnov test of normality [Affifi and Clark, 1984] indicated that the object manipulation data were non-normal (maxdiff = .958, P < .001). A modal point of zero rendered the data non-transformable, necessitating the use of a nonparametric procedure to investigate the group differences [Lehmann, 1975]. Therefore, a Kruskal-Wallis test for independent samples [Lehmann, 1975] was used, with means for each individual in each group cell.

The location scans at 15 minute intervals served as data points for the analysis of diversive exploration. To examine usage of the enclosures, maps of the usable, observable space of each enclosure were divided into approximately 6 × 6 m quadrats. Due to uneven-sized quadrats, the number of data points per quadrat were divided by the square footage of that quadrat to obtain comparable numbers.

Clumping in enclosure usage (i.e., habitual usage of only one or a few quadrats) was assessed by means of the coefficient of variation (CV) [Rasmussen, 1980]. The CV measures variability of usage, or clumping, by means of the following formula:

\[ \frac{\left(\sum (t - t_\mu)^2 / N - 1\right)^{1/2}}{t_\mu} \]

where \( t \) is the number of data points in the quadrat divided by the square footage of that quadrat, \( t_\mu \) is the sum of \( t \) divided by the number of quadrats in the exhibit, and \( N \) represents the number of quadrats in the exhibit.

A multiple regression of the predictive power of temporal and climatic variables on time spent in the most frequently used quadrats was conducted. The data met the assumptions of homogeneity of variance (Bartlett's = 78, n = 1,814, \( P = .961 \)) and uncorrelated error terms (Durbin-Watson statistic = 1.861, n = 1,814).

RESULTS

Specific Exploration

Figure 3 presents the mean amount of time spent manipulating objects over the course of the study, collapsed across subjects. As indicated by this graph, time spent...
in object manipulation was relatively low during the first few days in the habitats, increased rapidly, and then declined to essentially zero following approximately six months (180 days). A bivariate regression indicated a significant negative linear trend ($P<.001$, $B = -.140$, $\beta = -.606$). The number of days into the study accounted for approximately 37% of the variance ($R^2 = .367$). The two outliers during the latter part of the study are due to play involving object manipulation by juveniles.

The pattern of decline in object manipulation was similar across the three groups, but there were differences in degree. Group 1 exhibited more object manipulation than did the other groups. As shown in Table 2, the adult male in Group 1 was the only male to engage in a substantial amount of manipulation, with a mean manipulation time of approximately 30 seconds per 15 minute focal sample, compared to approximately 2 seconds per focal sample for the other two males. Similarly, the adult females in Group 1 exhibited more manipulation than did females in the other groups. Although there appears to be a difference among the groups, the results of the statistical test required by the distribution of the data indicate that the differences were non-significant (Kruskal-Wallis test statistic = 5.60, $df = 2$, $n = 3,3,3$, $P = .06$). However, this non-significance may be due to the reduction of data points required by the use of a nonparametric test rather than to effect size.

Object types receiving manipulation were also investigated. Objects which elicited the most manipulation were consistent across groups, with branches, sticks, browse, and bamboo responsible for the majority of manipulation in all groups; these objects together accounted for 66.96% of all manipulated objects.
TABLE 2. Mean time spent manipulating objects, by group (number of seconds per 15 minute focal sample)

| Subjects | Group 1 | Group 2 | Group 3 |
|----------|---------|---------|---------|
| Adult male | 29.64 (107.90) | 1.73 (24.86) | 2.25 (10.11) |
| Adult females | 50.30 (118.54) | 7.99 (33.82) | 17.44 (47.84) |
| Overall | 41.73 (105.56) | 15.07 (49.73) | 11.39 (47.44) |

“Diversive” Exploration

Percentage of enclosure entered. An analysis of the overall enclosure utilization revealed that no animal had entered all areas of its habitat during the time that it was observed. Figure 4 presents the percentage of quadrats entered by each individual following one year of occupation. As this figure shows, the subjects still had not explored up to 40% of the areas available to them. A preliminary analysis of related data suggests that the majority of unexplored quadrats were located on moderate or steep slopes, or were located next to water or moats.

Dispersal. Dispersal over the habitats was measured using the coefficient of variation (CV) [Rasmussen, 1980] (see Analysis section). The CV assessed the degree of variability of usage, in terms of clumping (high variability) vs. dispersal (low variability). A high CV (i.e., high degree of clumping) indicated that a subject spent the majority of his/her time in only one or a few quadrats. Low CVs demonstrated that a subject’s usage was more widely dispersed throughout the enclosure; a CV equal to zero would indicate completely random dispersal (i.e., equal usage of each quadrat).

Figure 5 presents graphs of the mean CVs over the year of the study for each family group. Individuals within a given harem group showed patterns more similar to each other than to animals of other groups; therefore, the mean of the CVs for individuals in each harem group was determined. All groups were highly clumped during the first quarter, showing dispersal only during the second quarter. Following six months of occupation, clumping then increased in all groups; with the exception of Group 1, enclosure usage became even more clumped during the last quarter of the year.

The quadrats next to the holding building received the majority of usage in all but two gorillas (i.e., more than 50% of location data points fell in these quadrats). These quadrats have concrete substrates and walls of solid concrete and wire mesh fencing. A multiple regression analysis was conducted to assess the predictive power of temperature, humidity, time of day, and number of days into the study on the amount of time spent in this quadrat. Humidity and time of day were significant predictors in Group 1 ($P<.05$), all four variables were significant predictors in Group 2 ($P<.05$), and time of day and day of study contributed significantly in Group 3 ($P<.05$). However, in only one of these groups did these variables predict a meaningful amount of the variance. Group 2 had an $R^2$ of .279 (i.e., 27.9% of the variance
was accounted for by these variables), compared to $R^2$'s of only .03 and .05 for Groups 1 and 3 respectively.

**DISCUSSION**

The purpose of this study was to investigate the pattern of adaptation of the gorillas to these novel habitats and to determine if habituation to the environments had occurred following one year on exhibit. It was expected that the subjects would at first exhibit a high level of exploration, gradually declining as a function of days in the enclosure. The present data did not completely conform to this expectation. Instead, the data indicated slow onset of exploratory behavior, a longer than expected period of stabilization of exploration, followed by significant declines. The slow onset of exploratory behavior is indicated by the initially low levels of object manipulation (see Fig. 3) and by high clumping during the first quarter of the study (see Fig. 5). The stabilization of exploratory behavior is indicated by the fact that object manipulation, once begun, did not decrease until six months into the study (see Fig. 3). Figures 3 and 5 demonstrate the dramatic declines in object manipulation and increased clumping seen in the third and fourth quarters. As an additional indicator of overall low exploration, a large portion of the exhibits remained unexplored for each subject; in the case of the males in Groups 2 and 3, this figure reaches a dramatic 40% (see Fig. 4). Finally, several of the animals (including the males in Groups 2 and 3, and one adult female in Group 2) showed virtually no object manipulation.
These results converge to suggest a period of initial caution, followed by limited exploration for approximately the first six months of habitation, that then declined fairly dramatically. Many potential explanations for these combined findings exist, including: 1) a lessened availability of objects to manipulate; 2) the continual novelty provided by naturalistic exhibits; 3) species-typical exploratory tendencies; 4) age of the subjects; 5) habituation, or a determination of functional utility; and 6) "neophobia," or fear of novel areas, or, possibly relatedly, inappropriate responses to such environments. Each of these explanations will be considered in turn.

**Lessened Availability of Objects**

One possible explanation for the dramatic decline in object manipulation was that preferred objects became less available. There is, however, no reason to suspect that the preferred objects of branches, sticks, browse, and bamboo decreased substantially in the exhibits over the course of the year. Browse and bamboo are daily introduced into the exhibits. Although the number of branches may have decreased as the gorillas dismantled saplings, this destruction should have resulted in a concomitant increase in the number of sticks. Thus, the declines in object manipulation were probably not due to the lower availability of manipulable objects.

**Novelty of Naturalistic Exhibits**

The long period of exploration could be due to the constantly changing nature of outdoor, naturalistic habitats. Seasonal changes, destruction and subsequent alter-
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ation of plantings, including replantings and the daily replenishment of foraging materials, all provide continually introduced novelty which may prolong exploration. As Paquette and Prescott [1988] demonstrated, a larger number of complex stimuli can increase the amount of time required for habituation. This could be supported by the lengthy period of exploration but is not totally supported by the increase in dispersal during the last quarter in Group 1.

Species-Typical Characteristics

Alternatively, low levels of object manipulation and slow dispersal may reflect species-typical temperamental characteristics. Gorillas are generally regarded as being less manipulative of objects than are chimpanzees and orangutans [Maple and Hoff, 1982], and tend to be active only during those portions of the day in which they are foraging [Jones and Sabater Pi, 1971; Schaller, 1963; Watts, 1988]. For example, Schaller [1963] states that wild mountain gorillas exhibited little object manipulation. Although anecdotal information regarding object use in captivity suggests that gorillas do manipulate objects [Maple and Hoff, 1982], the propensity of captive gorillas to manipulate objects has not been systematically studied.

Age

Alternatively, these results may be due to the individual difference of age, as eight of the 11 subjects in this study are over 20 years of age. A decrease in motor activity associated with age [Lapin et al., 1979] may be linked to the decrease in exploratory behavior. Additionally, older monkeys have been shown to require longer periods of time to adapt to novel stimuli [Cohen et al., 1979].

Habituation/Functional Utility

Declines in exploration may be due to habituation of the animals to the environments; that is, a desensitization to the novelty of the habitats. The relationship between exposure to stimuli and habituation is well-known, with exploration of stimuli often decreasing fairly rapidly following exposure [Hutt, 1967; Paquette and Prescott, 1988; Russell, 1983]. A “functional” hypothesis may be related to the habituation hypothesis; that is, the gorillas may have determined which locations have the most utility to them, and thus are not exploring additional locations. Exploratory behavior is presumed to provide the animal with information about the environment which is important for survival (e.g., foraging sites, resting sites, environmental hazards) [Birke and Archer, 1983]. Increased clumping and preference for the holding area quadrats may reflect that the animals have located those areas most useful to them, and have little need to venture beyond them. This would suggest that the animals are not necessarily unaware of the novelty the remaining unentered areas represent, nor are necessarily avoiding them, but that they are not compelled to explore those areas. This explanation is not supported by the increased dispersal seen in Group 1 during the last quarter.

Neophobia

Finally, the slow adaptation may reflect the previous housing conditions of these individuals. All of these gorillas have been reared in smaller, less complex environments than the present naturalistic zoo exhibits. Although these environments are ecologically appropriate for this species, these individuals have spent the majority
of their lives in simpler environments. These data therefore may indicate that the naturalistic environments are intensely novel to these subjects, and may reflect a kind of “neophobia” [Russell, 1983]. Neophobia may additionally account for the dramatic increase in exploration. The cessation in exploration may be due in part to an unwillingness to enter areas of heightened novelty; the remaining unentered quadrats may be unexplored because they possess aversive or unfamiliar characteristics (e.g., steep hills, or edges adjoining moats).

This hypothesis is consistent with findings of Renner [1987], who reported that rats raised in enriched environments showed greater amounts and diversity of object-related behavior than did subjects raised in deprived environments. Chimpanzees raised in restricted environments have also been found to be “retarded” in their responses to novel objects, although less so than rats [Menzel et al., 1963].

Several results of the present study support this neophobia hypothesis. First and foremost is the greater amount of exploratory behavior observed in those animals previously housed in a large outdoor area (Group 1). The other groups had previously been housed only in smaller, less complex, caged environments; we do not suggest that these environments were as restrictive as those in the studies described above [e.g., Renner, 1987; Menzel et al., 1963]; however, this experience may predispose the animals to feel more “comfortable” in a certain kind of environment. This greater amount of exploratory behavior is indicated by the fact that the animals in Group 1 spent more time engaged in object manipulation. (See Table 2; although this result was not significant, this may be due to the low power of the required test.) Furthermore, this group continued to show increased dispersal, or exploration, over the habitats, whereas the other groups showed increased clumping. Finally, Group 1 had entered a greater percentage of the available habitat, leaving an average of 17% unentered, compared with 26% and 23% for Groups 2 and 3, respectively.

The difference in exploratory behavior between groups is further demonstrated by differences between adult males and females in the different groups. The largest between-group disparity in unentered quadrats is found in males, with the male of Group 1 leaving 20% unentered, compared with 40% and 41% unentered in Groups 2 and 3. Additionally, as seen in Table 2, the males in Groups 2 and 3 show virtually no object manipulation, whereas the females in these groups do engage in this behavior, albeit not at the level of the females in Group 1. Similarly, the males in Groups 2 and 3 have entered a smaller percentage of the available quadrats as compared to the females, whereas the differences between the male and females in Group 1 are not as striking. These sex differences are suggestive of sex differences typically found following environmental restriction. For example, male rhesus monkeys (Macaca mulatta) demonstrate much greater inhibition of responses to novel stimuli than do females [Sackett, 1972], and this effect has also been found in other primate species [Mitchell, 1979].

In addition to the group differences, a finding in support of a neophobia hypothesis is the fact that in all but two individuals, the highest frequency of usage was observed in areas adjoining the holding building. This usage is meaningfully predicted by temporal and climatic factors in only one group, and even in that group a sizable amount of the variance remains unaccounted for. Russell [1983] distinguishes between novelty paradigms wherein subjects are placed in wholly novel areas vs. those in which subjects are given access to a new area adjacent to a familiar one. These holding area quadrats may represent more “familiar” environments to the animals. First, they have characteristics which are similar to the holding areas in
which the animals are both housed at night and in which they were held in quarantine prior to their release into the outdoor habitats. Additionally, these quadrats are representative of the housing experiences of the animals prior to their transfer to the zoo. This is true even in the case of Group 1; although these animals had previous experience in a large environment, the majority of their lives had been spent in less complex enclosures. Russell [1983] suggested that time spent in familiar areas represents a return to a “safer” zone; these data support such an interpretation.

Related to the neophobia interpretation, the present results may indicate that an active response to complex outdoor habitats is a learned phenomenon. For example, the individuals previously housed in the outdoor habitats have had the opportunity to “learn” how to manipulate natural objects and have adapted to the higher level of arousal that such novelty induces. Those animals that were not previously housed in such environments have not had this opportunity. Thus, a lack of exploration may not be due to “caution,” per se, but to an absence of previous opportunities to learn how to explore.

**Summary of Adaptation Findings**

There are alternative explanations to the adaptation findings. The group differences and preferences for quadrats with “familiar” characteristics lend support to the neophobia hypothesis. However, further study with these and other gorillas will provide better answers to this question.

The obvious possibility that these data could be explained by species-typical characteristics will continue to be tested as other zoos perform similar post-occupancy evaluation studies in newly completed gorilla exhibits, thus providing a concomitant increase in sample size, and with gorillas with differing rearing histories. Preliminary data utilizing the research protocol of this study with a new gorilla exhibit in Boston indicate much more immediate exploration and greater activity, even in adults (Schildkraut, personal communication, May 1989). However, the meaning of differences will be clarified as additional data become available.

If these patterns are due to habituation, or to a determination of the functional utility of the environment, further data on these subjects should reveal few changes in exploration. However, movement of groups among the enclosures (a management strategy planned in the future) should result in initial increases in exploration.

If the present results are due to either neophobia or to a lack of acquisition of skills related to exploring naturalistic environments, or to an interaction between the two, it may be expected that increases in exploratory behavior will occur in the future, as animals either become desensitized or as they acquire new responses to complex outdoor habitats. Information derived from studying the exploratory behavior of infants recently born in these exhibits may shed light on the effects of restricted environments. However, the tendencies of the individual infants may be superseded by the controlling role played by adult male gorillas [see Hoff et al., 1982]. Anecdotal evidence suggests that the males in the study groups effectively control the movements of the other animals in their groups; thus, if these adult males do not explore, they may limit exploratory behavior in developing infants.

This study does not provide definitive answers, but does provide further support for the effects of previous housing on enclosure usage and exploration. The results of this study, and others addressing the specific effects of physical environments on the behavior of captive great apes, will help us improve the effects of captive environments on reproduction.
CONCLUSIONS

1. It was expected that the subjects would at first exhibit a high level of exploration, gradually declining as a function of days in the enclosure. The present data did not completely conform to this expectation. Instead, the results converge to suggest a period of initial caution, followed by a period of limited exploration for approximately the first six months of habitation, that then declined dramatically. Potential explanations for these combined findings include: a) a lessened availability of objects to manipulate; b) the continual novelty provided by naturalistic exhibits; c) species-typical exploratory tendencies; d) age of the subjects; e) habituation, or a determination of functional utility; and f) neophobia, or possibly relatedly, inappropriate responses to such environments. Group differences and preference for quadrats with "familiar" characteristics lend support to the neophobia hypothesis, although further study with these and other gorillas is required.

2. These data suggest that areas which are familiar to gorillas, or representative of previous housing, may receive a large proportion of utilization, at least within the first year of habitation. This may be exacerbated if these familiar areas are those in which animals have contact with their caretakers. Consequently, this suggests an issue relevant to zoo design: that placement of familiar variables be made in areas visible to zoo visitors in order to allow the residents control over their environmental usage, while allowing for the recreation and education of zoo visitors.

ACKNOWLEDGMENTS

This work forms part of a master's thesis submitted by the first author to the Georgia Institute of Technology. The authors thank the Administration of the Yerkes Regional Primate Research Center of Emory University for the loan of these 11 gorillas. This work has been supported in part by NIH Grant RR-00165 to the Yerkes Primate Research Center, and by research grants from the Friends of Zoo Atlanta and the Atlanta/Fulton County Zoo, Inc., to the Georgia Institute of Technology. Additionally, we would like to thank Debra Forthman, Lori Perkins, Wendy Rogers, Beth Stevens, and three anonymous reviewers for their thoughtful criticisms of this manuscript, and Michael Bonar, Suzanne Elder, Wayne Esarove, Nadine Horowitz, and Wendy Wood for their careful data collection.

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