INFORMATION TO USERS

This material was produced from a microfilm copy of the original document. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the original submitted.

The following explanation of techniques is provided to help you understand markings or patterns which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting thru an image and duplicating adjacent pages to insure you complete continuity.
2. When an image on the film is obliterated with a large round black mark, it is an indication that the photographer suspected that the copy may have moved during exposure and thus cause a blurred image. You will find a good image of the page in the adjacent frame.
3. When a map, drawing or chart, etc., was part of the material being photographed the photographer followed a definite method in "sectioning" the material. It is customary to begin photoing at the upper left hand corner of a large sheet and to continue photoing from left to right in equal sections with a small overlap. If necessary, sectioning is continued again — beginning below the first row and continuing on until complete.
4. The majority of users indicate that the textual content is of greatest value, however, a somewhat higher quality reproduction could be made from "photographs" if essential to the understanding of the dissertation. Silver prints of "photographs" may be ordered at additional charge by writing the Order Department, giving the catalog number, title, author and specific pages you wish reproduced.
5. PLEASE NOTE: Some pages may have indistinct print. Filmed as received.

University Microfilms International
300 North Zeeb Road
Ann Arbor, Michigan 48106 USA
St. John's Road, Tyler's Green
High Wycombe, Bucks, England HP10 8HR

77-24,886

BROMLEY, Lyn Judith, 1948-
HORMONAL INFLUENCES ON THE SOCIAL STRUCTURE OF THE SQUIRREL MONKEY (*Saimiri sciureus*): IMPLICATIONS FOR THE EVOLUTION OF SOCIAL BEHAVIOR.

City University of New York, Ph.D., 1977
Zoology

Xerox University Microfilms, Ann Arbor, Michigan 48106

HORMONAL INFLUENCES ON THE SOCIAL STRUCTURE OF THE SQUIRREL MONKEY (*Saimiri sciureus*): IMPLICATIONS FOR THE EVOLUTION OF SOCIAL BEHAVIOR

by

Lyn J. Bromley

A dissertation submitted to the Graduate
Faculty in Anthropology in partial ful-
fillment of the requirements for the
degree of Doctor of Philosophy, The City
University of New York.

1977

This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

6/30/77
date

Warren G. Kinzey
Chairman of Examining Committee

6/29/77
date

Sydel Silverman
Executive Officer

Eric Delson, Ph. D.

Suzanne Ripley, Ph. D.

Leonard A. Rosenblum Ph. D.
Supervisory Committee

The City University of New York

Abstract

Advisor: Dr. Warren G. Kinzey

Primate social organizations are biological systems comprised of relationships between individuals. These relationships connote various degrees of attraction and repulsion of conspecifics and are the accumulation of numerous interactions or lack of interactions over time. The behavioral repertoire of the individual determines the interaction. Thus, it may be seen that hormones that affect the behavior of the individual also affect the interactions of the individual with conspecifics. The interactions affect the relationships and ultimately the social organization. Therefore, it is necessary to understand the affect hormones may have on discrete behavioral units and how if these units are altered they may affect the social organization.

The social organization of the squirrel monkey (<u>Saimiri sciureus</u>) is composed of subgroups of animals of the same age and sex. The principal subgroups are the adult females, the adult males, the subadult males and the juveniles. Social interaction occurs primarily within rather than across subgroups. Interaction between adult males and females is especially low in frequency. Observations on semifree-ranging groups (Baldwin 1968, 1971) and on laboratory groups (Coe and Rosenblum, in press) have indicated that the endogenous hormonal changes that occur during the annual breeding season are accompanied by changes in behavior and social organization.

In order to delineate the individual male and female behavior patterns that might be affected by gonadal hormones and thereby affect the social organization, four groups of Peruvian Saimiri were observed. Each group consisted of twelve monkeys, six male and six female. In Group 1 the females were ovariectomized and the males were intact. In the group designated 1H, the ovariectomized females were given a regime of depo-estradiol and the males were intact. Group 2 consisted of intact females and castrated males. Group 3 consisted of ovariectomized females and castrated males.

The degree to which each of the four groups exhibited the sexually segregated social pattern was extrapolated from inter-animal distance measures and from social behaviors such as "huddle," "contact" and "proximity." These measure indicated that the degree of segregation was different for the four groups. Groups 1 and 1H were the most segregated. Group 3 was the least segregated and Group 2 was intermediate. It is believed that these data indicate that gonadal hormones play a significant role in the maintenance of the sexual segregation of Saimiri. The absence of gonadal hormones affected the individual behavior patterns of the males and females thereby altering their interactions and consequently their relationships. The data also indicated that the sexually segregated social pattern is maintained by different social roles of the males and females and that gonadectomy may socially affect males more than females. Consequently the hormonal status of males may be more critical to the maintenance of or decrease in sexual segregation than that of the females. These data are considered from the perspective of understanding promate social organization as a biological system influenced by the ecology and phylogency of the species.

Acknowledgements

> "It is these teachers who have meant most to me
> in everyday life, as proven friends."
>
> Frederick Franck, 1976
> The Book of Angelus Silesius

I would like to thank Dr. Alphonse Riesenfeld for helping me to start on the path many years ago as a college freshman. The members of my dissertation advisory comittee, Doctors E. Delson, S. Ripley, W. Kinzey and L. Rosenblum have provided invaluable guidance and assistance. I would especially like to thank Dr. Warren Kinzey, committee chairman and my advisor at CUNY, for being patient and impatient at the appropriate times and for sharing his knowledge and insights with me. This work would never have been completed without his guidance.

This research could not have been accomplished without the skill and assistance of the staff of the Primate Behavior Laboratory, Downstate Medical Center, New York. Barbara Turner, Jayne Smiley, Gabe Sigerson and the men of the Animal Caretaking Service deserve special acknowledgement and thanks.

I would like to thank Alfie Rosenberger, fellow graduate student, friend, and ardent lunch-time debater for helping to clarify the issues and for sharing his insights with me. The advice, support, and companionship of Christopher Coe have been much appreciated gifts. Thank you for what we have shared. I would like to thank my parents for

their boundless support and encouragement.

Most of all, I would like to thank my research advisor, Dr. Leonard Rosenblum. Those of us who have had the good fortune to know him have been enriched by his intellectual achievements, his dedication to the pursuit of knowledge, his kindness, and his humor. I feel privaledged to have been his student and deeply appreciate his advice and friendship.

Lyn Bromley
June, 1977

"The meaning of life is to see"

Hui-Neng

TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

LIST OF FIGURES

CHAPTER ONE

INTRODUCTION AND RATIONALE

Man is a social animal, finding comfort and protection in living among others of his species. The nature of his sociality has puzzled and intrigued man for eons and he has looked beyond his own social group, his own culture in an effort to understand the mechanisms involved in and the reasons for being social. However, he has seen that the differences and similarities revealed by foreign societies are not enough to understand fully the nature of the social group and the social bond; because to spend a life as a member of a social network in a cooperative society is not the unique domain of Homo sapiens. Indeed it is not even a uniquely mammalian trait, but transcends phylogenetic lines occurring among insects, birds and fish. In order to truly understand sociality one must look not only beyond his own society but beyond his own species, especially to his closest relatives, the nonhuman primates. For it is among the monkeys and apes that the roots of man's sociality will be found. In their evolutionary legacy to us is the foundation on which uniquely human traits were laid.

The morphological history of the order Primates can be traced back some 70 million years. Recent studies of the fossil record reveal the divergence of our ancestors from the primitive eutherian stock into what we now recognize among living primates as the Strepsirhini and Haplorhini, (the tarsier, monkeys of the New and Old World and the apes). (See for example, Luckett, 1976).

Although not without its problems, the structural evolution of our order is reasonably well understood. Unfortunately those of us who have an interest in our social and behavioral heritage have less information available than our paleontologist colleagues. It goes without saying that neither social organization nor behavior leave any fossil record. However, within the strata is evidence of past ecology and adaptations. If we look to extant species, examine their behavior, their ecology and phylogeny and interpret what we see in terms of the fossil record, we may ultimately come to a clearer understanding of primate social organization as it evolved through time and exists today.

The interrelationship of phylogeny and ecology represents the key to such an understanding. This interrelationship has become the focus of investigations in the field and in the laboratory as revealed by the following quotations:

> However, in considering the relation between ecology and society it must be emphasized that each species brings a different phylogenetic heritage into a particular ecological scene. Consequently, one must consider not only ecology but also phylogeny in attempting to understand the evolution of primate social organization. The interrelations of these two classes of variables determines the expression of the character, in this case social structure. (Struhsaker, 1969, p. 113))

> It is necessary when studying primate behavior to consider which aspects of the behavior represent adaptations to the habitat and thus are paralleled by other, possibly distantly related, species living in the same habitat,

> and which aspects are peculiar to a given taxonomic group regardless of its habitat. (Chalmers, 1968, p. 278.)

> Cultural developments, like other modifications, are restricted by the phylogenetic heritage of the species, and phylogenetic adaptation itself proceeds slowly. Ecological correlations can put a premium on a certain type of society, but it cannot tell the species how to create such a society. Discussions of adaptiveness sometimes leave us with the impression that every trait observed in a species must by definition be ideally adaptive, whereas all we can say with certainty is that it must be tolerable since it did not lead to extinction. (Kummer, 1971a, p. 90.)

Observations of animals within their natural habitat is essential to understanding the relative contributions of phylogenetic and ecological forces in shaping social organization. The selective pressures exerted on a species can not be understood fully without detailed field analyses of diet, ranging behavior, competition with other species, predation, and habitat composition and fluctuation. These ecological variables are critically important to what we ultimately see as the social organization of the group.

In order to understand the role of phylogeny in shaping social organization the work of many scientists is required e.g. the systematist, the paleontologist, the evolutionary biologist, and the behaviorist. The role played by phylogeny in molding social structure relates to questions concerning the biological bases of behavior. These questions may be approached on two levels. Field observations reveal the natural behavior of the animal. Laboratory investigations enable certain behaviors seen in the wild to be analyzed and manipulated under controlled experimental conditions in an effort to delineate the underlying biological mechanisms, e.g. hormonal influences.

The social organization of the squirrel monkey (Saimiri sciureus) as described by Baldwin (1968, 1969) and Baldwin and Baldwin (1971, 1972) for both feral and semifree-ranging groups, consists of subgroups comprised of animals of the same age and sex. The principal subgroups are the adult females, the adult males, the subadult males, and the juveniles. Social interaction occurs primarily within rather than across subgroups. Interaction between adult males and females is especially low in frequency. This social pattern is maintained in the laboratory (Coe and Rosenblum, 1974, and in press; Fairbanks, 1974).

As indicated above, hormones are important mediators of behavior. Observations of Saimiri living as semifree-ranging groups (Baldwin, 1968, 1971) and as laboratory groups (Coe and Rosenblum,in press) have indicated that the endogenous hormonal changes that occur during the annual breeding season are accompanied by changes in behavior and social organization. Other laboratory research (Alvarez, 1969; Coe and Rosenblum, 1974) has also indicated that gonadal hormones may play a significant role in the development and maintanence of the adult isosexual groupings described previously.

The influence exerted by hormones on behavior has been the subject of many investigations including the one presented herein on the squirrel monkey. The purpose of this study was to delineate the effect of gonadal hormones on the individual behavior patterns of Saimiri males and females. It is a basic hypothesis of this research that hormones affect social organization by influencing the behavior of the individual and thus that individual's interactions with other animals. The influence exerted on these interactions ultimately influences relationships with other individuals, and social organization is comprised of relationships. (Hinde and Stevenson-Hinde, 1976.)

In order for the data to be viewed in the larger perspective of the evolution of social behavior, the following presentation is a discussion of the systematic nature of social organization, the effect of ecology and phylogeny on social organization, and the influence of hormones on behavior. These variables will then be considered in relation to the social organization of Saimiri.

CHAPTER TWO

GENERAL BACKGROUND

Social Structure and Systems Theory

Social structures are in fact social systems. As such they are best understood from the perspective of systems theory, as possessing the characteristics of biological systems. Thus, they are complex, multilevel, and goal-directed (von Bertalanffy, 1950; Laszlo, 1972; Mesarovic, 1968), none of which implies conscious intent nor teleology. In order to make this clear, we may substitute the word function for goal. Biological systems doubtless perform functions. To illustrate by analogy consider the locomotor system. It, too, is complex, multilevel and goal-directed in that the muscles, bones, motor neurons, cerebellum, motor cortex, etc. represent subsystems that function in concert to produce movement; such that the animal is mobile within a given environment in the most efficient manner possible. Mobility (i.e. movement) is the ultimate goal although the muscles, bones, etc., each with their own particular goal-function, have no notion of this per se. Each subsystem can be separately viewed and analyzed. Yet it is only when our knowledge of the cortico-cerebellar pathways, the lever mechanics of muscle and bone, and the contractile properties of actin and myosin is viewed as a whole can we begin to understand fully the physiology and mechanics of movement, although not the biological role as discussed by Bock and Von Wahlert (1965).

The ultimate goal-function of social organization is to mediate the life processes, e.g. eating and reproducing, in the most efficient manner possible. This view is shared by Crook et al. (1976, p.262):

> We argue that particular social structures arise because they provide an optimal context within which the individuals comprising them carry out vital functions.

The social system can then be seen to be comprised of individually analyzable subsystems each fulfilling a "vital function," i.e., each with a specific goal. Again, we may turn to Crook et al. (1976, p. 262) to explicate this point:

> We analyze social structure here in terms of sub-systems within which individuals achieve the main vital functions.

Biological systems, be they social or physiological, are essentially open, self-regulating and equifinal (von Bertalanffy, 1968; Laszlo, 1972). The latter two components can be seen to be consequences of the first. An open system has requirements that a closed system does not. It functions differently. A closed system moves toward either entropy or equilibrium, as opposed to maintaining a steady state, i.e., homeostasis. An open system does not move toward entrophy or equilibrium because there is a continuous inflow and outflow, a building up and a breaking down. As defined by von Bertalanffy (1950, p.23):

> A system if closed if no material enters or leaves it; it is open if there is import and export and, therefore, change of the components. Living systems are open

> systems, maintaining themselves in exchange of materials with the environment, and in continuous building up and breaking down of their components.

It follows that primate societies, as biological systems, are open systems in exchange with the environment. Membership changes through birth, death, emigration and immigration. We must remember at this point that the system is goal-directed, the goal being "to mediate the life processes in the most efficient manner possible." The coupling of this goal with the property of exchange necessitates self-regulation (e.g. regulation of reproduction, and resource exploitation). There must be a method to regulate relationships and behavior between group members, i.e., some form of communication. There must be a method to incorporate new group members, for example through socialization.

A system could not exist where the processes of exchange and buildup were random. Open systems are structured wholes, performing specific functions in relation to specific surroundings, thus necessitating ordered self-regulation. Implicit here is the notion of adaptation, a key concept in the understanding of social systems. The social group is a medium through which animals adapt to their environment.

The third characteristic of biological systems, that of equifinality has a very special meaning for investigators of social systems. It is the concept of equifinality that enables us to understand the variability in the diverse primate social groups. Equifinality is defined by von Bertalanffy (1968, p. 131).

> In any closed system, the final state is unequivocally determined by the initial conditions....This is not so in open systems. Here, the final state may be reached from different initial conditions and in different ways. this is what is called equifinality, and it has significant meaning for the phenomena of biological regulation.

The significance of equifinality to our discussion resides in the fact that various configurations of subsystems and regulatory mechanisms can result in the attainment of the same function-goal. In an open system a perfect correlation between a particular end and a given mechanism rarely exists. When one applies the concept of equifinality to the fact that all species living in similar environments do not have the same social organization the variation is less perplexing. One can say that the species developed their particular social organizations along different phylogenetic avenues and consequently have made slightly different adjustments and adaptations in the various subsystems and regulatory mechanisms along the way.

A final and particularly important point concerns the hierarchal nature of subsystems. von Bertalanffy (1968) and Crook *et al*. (1976) suggest that certain subsystems may be more critical than others to the final configuration of the total system. Certain subsystems and characteristics may be less malleable than others, e.g., reproductive mechanisms.

Since the nature of social organization is truly that of a system, it functions as a system, has evolved as such, and should be investigated and analyzed within that perspective. Therefore a discussion of the types of social structures in the order Primates should include a discussion of systems and subsystems. Systems theory enables the investigator to conceptualize beyond the classification of groups as multimale, unimale or harem. In addition to such classification schemes, we can explore subsystems such as rearing, mating, resource-exploitation, and predator avoidance. As discussed by Crook et al. (1976, p. 262):

> The division of a society into functional sub-systems is useful analytically in that it helps to focus attention on environmental variables and species parameters which are likely to be particularly important in the accomplishment of a particular function, but which may have little influence on the accomplishment of others. For instance, one species parameter, the maturation rate of the young, provides critical constraints on the structure of the mating and rearing subsystem, but may be less critical in determining the structure of the resource exploitation group. It must be remembered however, that these subsystems do not exist in isolation but are fully integrated and that individuals usually operate within several subsystems simultaneously.

The constraints that the particular characteristics of a species on subsystems or that one subsystem may impose upon another are in fact the accumulation of millions of years of constraints which occurred as the species evolved, incorporating new characters, loosing old ones, and adapting to new environmental variables. The subsystems must be viewed not only in the here and now of functional biology but must also be approached from an evolutionary-time perspective. The "here and now" understanding indicates the importance of ecological variables in shaping social structure and the evolutionary perspective addresses itself to the importance of phylogeny. The concepts of equifinality and a hierarchy of subsystems are particularly important for understanding the complex interplay of ecology and phylogeny in shaping social systems.

Primate Social Structures

Investigations of primate social life have revealed it to be varied and complex. In an effort to categorize and classify the array of social structures within the order, investigators have relied primarily on head counts of adult males within the group. The emphasis on the number of males within the group developed in conjunction with a preoccupation on the multimale group as model for the order. Indeed, for some earlier investigators the existence of unimale groups could only be explained by adaptations to aberrant primate habitats. This view was later challenged. (Gartian, 1968; Eisenberg et al., 1972). As stated by Eisenberg et al. (1972, p. 866):

> This tendency to characterize most primate species by a multimate social structure and to set aside those species exhibiting unimale groups as cases of adaptation to extreme environments was motivated in part by a desire to emphasize the uniqueness of primate societies when contrasted with the social groupings of other mammals.

The early bias toward multimale groups was also strongly influenced by the thinking and expectations that stemmed from the early concentration on the behavior of macaques and baboons. This papionin species orientation has diminished in recent years as our knowledge of other primates has increased.

The preoccupation with the multimale group also led to an emphasis on the study of male behavior (male dominance, male tolerance, male aggression) reflecting the erroneous belief that it is the male that determines the social organization. In fact, neither males nor females solely determine the nature of the social system. It is the totality of male-male, female-female and male-female relations that is the determinant. The role of females as well as males in determining the social system is clearly evident in pair-bonded species. As reported by Epple (1970, 1973) and Rothe (1975), female as well as male marmosets (Callithrix jacchus) exhibit a considerable degree of intolerance for conspecifics of the same sex. In captive animals maintained in hetersexual groups instead of pairs, the female who emerges as dominant will harass the subordinate females until they are incapable of reproducing. This kind of sterility is the result of social stress and has been reported in other mammals (Christian, 1970). Mason's (1974, 1975) work on partner and social preferences in Callicebus moloch is also indicative of female as well as male roles in shaping social structure. A field study on C. torquatus torquatus (Kinzey et al, 1977) indicated that the adult male and female pair shared leadership of the group. The female primarily acted as leader while the male appeared to direct group activity. The importance of the female in the maintenance of the social group can also be seen in multimale troops where rank, one measure of dominance is transmitted matrillinealy and where females are more often the primary socializers of infants (Koyama, 1967). The issue here is not only to indicate the importance of female roles nor simply to emphasize females as essential social elements but rather to look at the behaviors of both sexes as reflective of the regulatory aspects of the system. Primate females are not the passive recipients of a male-determined social order. The perpetuation of a structure can only be accomplished by the participation of all its constituents. Therefore we must view social organization as more than demography, especially more than male demographic trends, and look for the roles fulfilled by males and females of all ages.

There is no particular social organization that is the "norm" for primates, not even gregariousness. Instead, we see that the primates, similar to other mammalian orders, exhibit diverse social organizations which reflect both the varied environments in which they live and their phylogenetic histories. Ecological variables impose constraints on organization and these in turn must come to a "compromise" with internal constraints imposed by the animal's biology, i.e., its physiology and morphology. In 1966, Crook and Gartlan, in an attempt to delineate the important ecological determinants of social organization, categorized habitats and correlated these zones with certain organizational types. Gartlan (1968) and Eisenberg et al. (1972) refined this approach. The following descriptions of the social groups are based on the works cited above with certain revisions. The harem system is considered as a specific pattern separate from the unimale group and the multimale pattern is subdivided into three rather than two types. Primate social groups fall into five general patterns: solitary, pair-bonded, unimale, harem and multimale. Each pattern may appear to be based on demography only but in fact each represents a unique configuration of social relationships and features.

Solitary Species

The solitary pattern is found primarily among nocturnal primates, e.g., the lorisoids and some lemuroids. Lone adult males and females with immature young maintain individual territories. Social interaction between conspecifics is typically infrequent and male-female interaction is fairly limited, occurring mainly during the mating period. However the data provided by Charles-Dominique (1972, 1974) and Martin (1972) indicate that the "solitary" species may not be as asocial as the name implies. Among the strepshirhine species exhibiting this social pattern, the females tend to be more aggregative than the males and even the males have some social contacts. These investigators also report that female cheirogaleines and galagines share all or part of their territories with other females and _Microcebus_ females actually share nests. However, foraging is always a solitary activity.

The territories of the individual males are a mosaic superimposed upon those of females. Dominant males maintain territories contiguous and overlapping with those of females whereas subordinate males do not. Charles-Dominique (1971) reports that subordinate Galago males share territories and form what he calls "vagabond" groups, commonly referred to by other authors as bachelor bands. A rise in rank, resulting in the acquisition of a territory, seems to obliterate whatever affiliative behavior occurs among the males. A male will typically defend his own territory and that of his females' whereas a female will defend only her own. Galago females are dominant over males and Charles-Dominique reports that female aggression toward males during mating is not uncommon. Male-female affiliation is indicated by grooming.

It is the contention of Charles-Dominique (1974), Martin (1972), and Eisenberg et al. (1972) that this solitary pattern represents the ancestral social condition for primates. The sociality of these solitary primates is considered by these authors to reflect some basic tendencies within the order, i.e., females are more aggregative than males and males are relatively intolerant of one another especially when access to adult females is at stake. If we do accept the notion of the solitary pattern as basal for the order it is important to note the behavioral changes and specializations that have occurred in the other social organizations, e.g. heightened female intolerance in pair-bonded species in contrast to the greater development of female cohesiveness in other types of social groups, and increased male tolerance in multimale systems.

Pair-Bonded Species

The pair bonded pattern is found in the New World among the Callithricidae, *Callicebus*, and *Aotus*. The Old World primates exhibiting this organization include the Hylobatidae, *Indri*, *Avahi*, *Lemur mongoz* (Sussman and Tattersall, 1976) and *Presbytis potenziani* (Tilson and Tenza, 1976). The social group typically consists of an adult male and female pair and their immature offspring. Subadult progeny may be excluded from the group by the parents (Carpenter, 1940). As mentioned previously there is a considerable degree of male-male and female-female intolerance. Mason (1974, 1975) has indicated that in *Callicebus moloch* attraction bwteen male and female is much greater than attraction between members of the same sex. Hostility and aggressiveness toward same-sex conspecifics may be directed towards offspring once they reach the subadult stage, i.e., become sexually mature. Aldrich-Blake and Chivers (1973) witnessed the increasing aggressiveness of an adult male siamang towards his subadult son, ultimately forcing the young *Symphalangus* to leave the group. He was later joined by a young female who may have been expelled from her group by her mother. The frequent calls of expelled gibbons and siamangs are considered by Aldrich-Blake and Chivers to be attractants for the opposite sex, enabling lone inidviduals to locate each other. New groups are frequently unstable. In the case cited above a second female later joined the pair, subsequently left, and then returned and left again.

It is possible that a birth may be the required stimulus for stability within the group.

New World pair-bonded primates exhibit a great deal of paternal behavior. They regularly carry the infants and transfer them back to the mother for nursing. Moynihan (1976) reports that marmoset familites are quite cohesive, rarely wandering out of easily communicable distance. Symphalangus males are also extremely paternal, carrying the young and assisting them over particularly difficult crossings (Chivers, 1972). The degree to which other pair-bonded males are paternal is still unclear. According to Eisenberg *et al*, 1972, the gibbons and *Indri* are not extremely paternal and reliable data on *Avahi* and *L. mongoz* paternal behavior is unavailable.

Although the reason for the correlation is not yet fully understood, sexual dimorphism *via à vis* body size is negligible among monogamous pairs. The low level of dimorphism may be related to the fact that both males and females engage in visual and vocal displays, (duetting) directed toward adjacent groups. These displays function not only as territorial behaviors but may also solidify the pair bond and protect the social integrity of the group (Ripley, 1967; Tilson and Tenaza, 1976). Chivers (1972) and Aldrich-Blake and Chivers (1973) also describe female hylobatids as active in the leadership of the group.

The considerable degree of paternal behavior exhibited by New World pair-bonded species, although not yet confirmed in other pair-bonded males, has been attributed to parental investment theory (Trivers, 1972). The supposition is that the male "realizes" that the offspring are his genetic investment and acts to protect it. However, before we accept this as a universal explanation of pair-bonded species we should investigate other factors which may contribute to this behavior pattern. For example, female callithricids, (whose genetic investment is no less than the male) exhibit early rejection of the young (Epple, 1975). This may or may not lie in the fact that the female exhibits a postpartum estrous. The endorcrinological and behavioral changes of the postpartum female should be investigated to help clarify the issue.

Unimale Species

A unimale group is composed of several adult females, their immature offspring, subadult females and one adult male. Among the primates exhibiting this social structure are all the species of the genus _Ceropithecus_ (except _C. aethiops_), the closely related _Erythrocebus patas_, _Presbytis senex_, the Dharwar _Presbytis entellus_, and the _Colobus guereza_. All male bachelor bands and solitary males also occur in these unimale species. Solitary males are apparently more common among the forest dwelling than the open country primates. Thus, solitary _Cercopithecus_ are commonly reported (Struhsaker, 1969) whereas in contrast one finds patas and langur males in bachelor bands (Hall, 1965). Despite the occurrence of bachelor bands, male-male intolerance in bisexual groups of these species is typically great as exemplified by the work of Kummer (1974). E. patas males which were placed in an arena as pairs immediately fought and continued to fight until a winner emerged. The dominant E. patas male relentlessly harassed and pursued the subordinate until he was near death. The apparent lack of a signal of submission in E. patas may partially account for the intolerance and sustained harassment.

Although the E. patas male is aggressive toward other males, he is not dominant over the females of his group. Crook (1970) reports that Hall felt that "the initiative in keeping a particular male in the group may come from the females." (p. 135) In fact the son of the highest ranking female may succeed to leadership in the group by virtue of his mother's dominance.

The role of E. patas male as described by Hall (1965) is extremely periphearal. He shows little interest in his offspring and does not demonstrate any overt paternal behavior. The females are aggregative and appear to form the main social group. They have a strong dominance hierarchy and female coalitions against the male are not uncommon. The male's primary social role seems to involve staving off forces that threaten the group. His reproductive role is obvious.

Obviously the male-male, female-female and male-female relations in the three organizational patterns described so far vary considerably. They culminate in very different organizations and reflect basic differences in behaviors related to attraction and repulsion of conspecifics.

Harem Species

The harem species are usually classified as unimale. However, differences in the underlying social relations, specifically the male-male interactions, indicate the need for separate consideration (Kummer _et_ _al_., 1970; Rowell, 1972). As reported by Kummer (1971a), _Theropithecus_ _gelada_ and _Papio_ _hamadryas_ _hamadryas_[1] are harem species and possibly _M_. _sphinx_ (Jouventin, 1975). A troop consists of many males, females and progeny ranging from infancy through subadulthood. These troops are subdivided into harem units composed of one adult male, several females and immature young. Breeding occurs exclusively within these one male units.

In the case of the hamadryas baboon three levels of organization exist within the herd. First, there are the one male breeding units, several of which are organized into the second level, the band. The largest level of social organization is the troop which is composed of several bands. The baboons may forage as a harem, a band, or much less commonly as a troop. In fact, the "troop" functions as a sleeping aggregation while the harem and the band are the units within which most social interaction occurs.

---

[1] According to E. Delson (personal communication) five major subspecies not species of _Papio_ should be recognized. They are _Papio_ _hamadryas_ _hamadryas_, _P_. _h_. _ursinus_, _P_. _h_. _anubis_, _P_. _h_. _papio_, and _P_. _h_. _cynocephalus_ (see Jolly and Brett, 1973). In this paper Delson's classification is recognized.

The gelada troop does not exhibit the same three levels of social organization. The functional social units are the harems and the troop. Hamadryas-like bands do not exist although kinship clans, similar to those reported for Macaca nemestrina (Rosenblum, 1971), are recognizable (Gartlan, 1973). Kummer's field and laboratory work (1968, 1971b, 1973, 1974) suggest that the nature of male-male aggression, attraction and cooperation in gelada and hamadryas is significantly different from that of unimale species (cf., Erythrocebus patas). For example, two gelada males introduced into the same experimental situation as the two previously described E. patas males exhibit a very different response. Initially, they also fight. However, as soon as a winner emerges, hostility ceases. The subordinate male indicates his submission by presenting, the dominant male responds by mounting, and affiliative behavior commences. Afterwards, the males mutually groom, walk together and interace peaceably.

Hamadryas males do not challenge each other over females that are already "possessed" (Kummer, 1968, 1973). In the wild young males without harems often attach themselves to a harem leader. This young male acts cooperatively with the older adult male but does not engage in sex with the latter's females. Another example of the interactive relations between males is that hamadryas males belonging to the same band act in concert against group threats and in choosing daily routes. They recognize dominance realtionships and respect, without challenge, the possession of females by subordinate males.

Hamadryas males, unlike patas males, show interest in the young and are quite paternal towards both male and female juveniles. A young hamadryas male may exhibit a special interest in juvenile females whom he may "kidnap" and care for as a foster parent until the females reach sexual maturity; at which point they begin to mate. This kidnapping behavior is the social mechanism by which new harems are formed.

The males of the unimale species, when compared to the males of the harem species, can be seen to differ greatly in the degree of affiliation, cooperation and tolerance exhibited towards other males. They also differ significantly in their relations with females and younger animals. The differences in these social relationships are fundamental to the differences in the social organization of the troops, and are manifest in and maintained by the differences in the behavioral repertoires of the respective species. The greatest (and in fact over-emphasized) similarity between unimale and harem species concerns the breeding exclusivity of the adult males.

Multimale Species

The multimale pattern is found among diverse species of the New and Old World. As the name implies multimale species live in groups composed of many adult males, females and immatures of all ages. Breeding is not the exclusive right of one adult male. Dominance rank may or may not influence a male's ability to mate successfully (Rowell, 1974). In some species an estrous, and occasionally a nonestrous female may form a consortship with a male for several days. In others, the consortships may last several hours or only minutes. Male-male relations are equally variable within this category. In general, all multimale species exhibit a greater degree of male-male tolerance and affiliation than do the males of the unimale and harem species. However, the magnitude of the tolerance and the quality of the male-male relations is the basis for subdivisions within this category.

1) General Multimale

In the general multimale system male-male relations appear to be more integrated and relaxed. This is a generalization, however, and should not be taken to mean that all general multimale species exhibit identical social relationships. There is considerable variation evident in dominance, mating, the effect of dominance on mating, male-female relations, and the relationship of adult males toward infants and juveniles. Inter-specific comparisons of the genus *Macaca* illustrate the variability possible within the framework of the multimale system. For example, rhesus males (*M. mulatta*) display minimal interest in infants and juveniles (Kaufman, 1967; Sade, 1965; Southwick *et al.*, 1965) whereas bonnet males (*M. radiata*) frequently play with and are paternal towards juveniles (Simonds, 1965). *Macaca sylvanus* represents an extreme in the amount of paternal care directed towards infants and juveniles, carrying young animals away from their mother, playing with them and encouraging their locomotor skills (Burton, 1972; Crook, 1970). The male involvement with infants and juveniles exhibited by the barbary ape (M. sylvanus) is exceeded only by that of males of pair-bonded species. The differences among macaque males in this social relationsip reflect organizational differences and adaptations which are also manifest in the relationships between males, males and females, and females and females.

Mating behavior also varies from one macaque species to another and throughout the multimale primates. Male and female rhesus monkeys may form exclusive consortships that last for several days (Carpenter, 1942). Bonnet macaques, on the other hand, do not establish consort relations and mate promiscuously (Simonds, 1965). Females may copulate with up to seven males in one day. The formation of temporary male-female consort relations is also seen among the forest-dwelling multimale baboons the Papio "cynocephalus" group (Rowell, 1966; Ransom and Rowell, 1972). However, the consort relations differ somewhat from those seen in the rhesus macaque and, according to Ransom and Rowell, reflect a social bond between the male and female that extends past the copulatory period.

The social relations between males and females also vary from species to species. In general the macaques and baboons exhibit a greater degree of male-female affiliation and integration than do the multimale *Presbytis entellus* groups (Jay, 1965; Ripley, 1967). In addition, langur males exhibit little interest in infants. The females form a cohesive subgroup in which interest in infants is very high and babies are regularly passed around for inspection and fondling. *Presbytis entellus* where it occurs as multimale, is probably an age-graded as opposed to a general multimale species (see below). However, *P. entellus* is quite labile and does not exhibit a species specific social structure.

A thorough discussion of the range of variability among the multimale species is beyond the scope of this paper. However, the examples cited illustrate some of the differences that do exist and also indicate that social organization cannot be considered solely on demographic grounds.

2) Age-Graded Multimale Species

Age-graded multimale species exhibit less male-male tolerance than do general multimale species and, as the name implies dominance and age are correlated. Therefore, there is usually a mature male functioning as troop leader, as may be seen among the mountain gorillas (*Pan gorilla*) (Schaller, 1963) and the pig-tailed macaques (*M. nemestrina*) (Bernstein, 1969). There is of course variation among the age-graded species and not all exhibit identical social relations. Eisenberg *et al*. (1972) consider the male-male relations in the age-graded system to be less integrated and more influenced by dominance status. However, male-male tolerance is greater than that of the unimale groups.

3) Segregated Age-Graded Multimale Species

The Old World monkey Miopithecus talapoin and the New World Saimiri sciureus represent a departure from the multimale structures discussed so far. As reported by Gautier-Hion (1971), Rowell (1973) and Baldwin (1968, 1971), the males of these species are organized into a social heirarchy that is based on age classes; however, no male emerges as the strong, dominant troop leader. Male-male tolerance is moderately high but female-male tolerance is very low. Social interactions between the sexes, other than mating behaviors, are minimal. This social structure will be discussed in greater detail in the section on Saimiri.

A variation and possible subdivision of the segregrated, age-graded multimale system is represented by the social organizations of Lemur catta and Propithecus verreauxi (Jolly, 1966). They do not associate in a sexually-segregated structure which is exactly like that of the talapoins or squirrel monkeys; however, there are similar organizational features. These strepsirhine groups are organized around a female matriarchy and the males may be considered subordinate to the females. Thus, the male-female interactions and relations appear to be closer to the segregated system than to the other types of social groups. It should be noted that Richard (1974) has indicated that the sexual composition of P. verreauxi groups is more variable than originally seen by Jolly (1966). However, the dominance of the females was confirmed.

Each organizational category represents a unique configuration of social relations that form the foundation and cement for differences in mating and rearing strategies. The behavioral repertoires of the species, especially the differences in behavior which are related to the attraction and repulsion of conspecifics, are in turn the building blocks of the social relations we see as varying throughout the order. The existence of different social roles has been related by Gartlan (1968), Rowell (1972) and Crook et al. (1976) to ecological variables. Various ecological conditions place specific functional demands on the group.

Ecological Influences on Social Organization

It is argued that the environment in which a species lives influences the type of social organization exhibited by exerting specific functional demands on the group. The nature of the myriad of ecological and social relationships is extremely complex and efforts to correlate the pertinent variables have been extensive (Clutton-Brock, 1974; Gartlan, 1968; Struhsaker, 1969, 1975; Crook and Gartlan, 1966; Eisenberg et al., 1972). The following discussion represents an extremely brief review of the most salient ecological influences on primate social groups. It is by no means definitive or exhaustive, but rather illustrative of the complexity of the issue. Crook and Gartlan, ln 1966, outlined broad ecological zones and correlated these zones with types of social structures. In 1972, Eisenberg et al. revised this approach. Both attempts relied on defining environmental variables in terms of general habitats, and-trophic preferences e.g., that of forest-dwelling frugivore. This approach met with some criticism (Aldrich-Blake, 1970; Clutton-Brock, 1974; Moynihan, 1973; Struhsaker, 1969). The core of the criticism is indicated by the following quotation:

> What features of social organization consistently correlate with the rain forest habitat? Our studies in the Kibale Forest and elsewhere show that there are few correlations. (Struhsaker,1975).

The problems lie in the difficulties inherent in generalizing. Species do not simply adapt to a broad ecological zone, rather they adapt to a niche within the larger habitat. This view is supported by Kummer's (1971) contention that social organizations can not be considered as "simple correlates of simple classes of habitats." This statement does not negate the influence of the environment on social organization, rather it is indicative of the multifaceted nature of the relationship. (Ripley 1970).

The complexity of this issue is indicated in Table 1, which is a modification of the classification presented by Eisenberg _et al_. in that the harem species are listed separately (1972). In support of the preceding statements, one can see that the arboreal forest-dwelling frugivores live as age-graded multimale groups (cf., _Ateles_, Klein and Klein, 1975), as unimale groups (cf., _Cercopithecus ssp_, Strunsaker, 1969), and as monogamous pairs (cf., _Hylobates_, Chivers, 1972). Folivorous species are equally variable. _Presbytis entellus_ lives as age-graded multimale or unimale

Table I: Distribution of Social Organizations and General Feeding Ecologies for Selected Species (modified from Eisenberg *et al.*, 1972).

SOLITARY	PAIR-BONDED	UNIMALE
Insectivore-frugivore	Frugivore-Insectivore	Folivore-arboreal
Lemuridae:	Callithricidae:	Colobinae:
Microcebus murinus	*Callithrix jacchus*	*Colobus guereza*
Cheirogaleus major	*Cebuella pygmaeus*	*Presbytis entellus*
	Saguinus oedipus	*Presbytis senex*
Lorisidae:		
Loris tardigradus	Cebidae:	Frugivore-arboreal
Galago demidovii	*Aotus trivirgatus*	
Perodicticus potto	*Callicebus moloch*	Cercopithecidae:
		Cercopithecus
Folivore	Folivore-frugivore	(*ssp* except *C. aethiops*)
Lemuridae:	Indriidae:	Omnivore-terrestrial
Lepilemur mustelinus	*Indri indri*	
		Cercopithecidae:
	Hylobatidae:	*Erythrocebus patas*
	Hylobates lar	
	Symphalangus syndactylus	

HAREM	MULTIMALE	AGE-GRADED MULTIMALE
Omnivore-terrestrial	Frugivore-omnivore-semi-terrestrial	Folivore-arboreal
Papionini:		Colobinae:
Papio hamadryas hamadryas	Cercopithecini:	*Presbytis entellus*
Theropithecus gelada	*C. aethiops*	
		Cebidae:
	Papionini:	*Alouatta palliata*
	Macaca mulatta	
	Macaca radiata	Frugivore-arboreal
	Macaca sylvanus	
	P. h. anubis	Ceboidea:
	P. h. ursinus	*Ateles geoffroyi*
	P. h. cynocephalus	*Saimiri sciureus*
	Pongidae:	Cercopithecidae:
	Pan troglodytes	*Miopithecus taloapin*
	Folivore-arboreal	Folivore-frugivore-terr.
	Colobinae:	Pongidae:
	Colobus badius	*Pan gorilla*

depending upon the aridity of the environment (Jay, 1965; Ripley, 1967; Yoshiba, 1968). Presbytis senex and Colobus guereza are unimale; Colobus badius is multimale; and Alouatta is age-graded multimale (Clutton-Brock, 1975; Struhsaker, 1975; Eisenberg et al., 1972).

A broad adaptive zone (e.g. rainforest) consists of many niches, each of which encompasses different combinations of ecological variables. Several ecological variables are outstanding in terms of the degree of impact and constraint they have upon social organization: (1) density of resources, (2) seasonal fluctuation of resources, (3) spatial distribution of resources, and (4) extent of predation. These vary across zones, e.g., scrub savanna is generally less bountiful than a forest environment. Therefore, savanna demands are usually different than those of the forest. As mentioned above, niches within zones combine these variables in any number of ways.

Some generalizations are possible. For example, species that live in arid country, usually have a much lower biomass than species living in moist environments. Thus patas monkeys and hamadryas baboons have a population density of 0.6 animals/km^2 and 2.0 animals/km^2 respectively whereas forest-dwelling baboons in Uganda exhibit a density of 11.0 animals/km^2 (Jolly, 1972). The availability of resources appears to be a limiting factor for the respective populations. The reduction of population density in response to harsher environments can also be demonstrated by comparing savanna chimpanzees with their forest-dwelling counterparts, 1.0 animal/km^2 as compared to 7.0 animals/km^2 (Jolly, 1972). A decrease in the population density of a species can occur through an increase in the size of its range or by a reduction in the size of its groups or through a combination of the two. Whether a species exhibits one alternative or the other depends upon the other ecological pressures present in the environment. Reduction of group size can also be accomplished in more than one way, e.g., a large multimale group can become a unimale group. Again, the other ecological variables at work in the habitat influence the alternative.

The field work of Clutton-Brock (1974) on _Colobus badius_ and _Colobus_ _guereza_ illustrates the relationship between diet, resource distribution and social structure. _C_. badius lives in large multimale groups which have an extensive home range. _C_. _guereza_, on the other hand, lives in small unimale groups with a small home range. Both are arboreal, forest-dwelling folivores, yet ecologically they are quite different. Although a folivoare, _C_. _badius_ does not eat mature leaves. Its feeding is selective (e.g. buds and shoots) and the food is available seasonally in different areas of the home range. This selectivity in diet necessitates the location of the sources of unevenly distributed foods. In contrast, _C_. _guereza_ eats more mature leaves which are a more evenly distributed, less scattered resource, and therefore, easier to locate. According to Clutton-Brock the dietary difference between these two species, with the concommitant difference in resource density and distribution, results in the vastly different social structures exhibited by both. A diet which is dependent on clumped, unstable food sources requires a large home range in order to incorporate enough resources, and also a large group to spread out and help locate them (Ripley 1970). Conversely, evenly distributed resources enable a group to be smaller since the location of food is less difficult. Thus, the home range does not have to encompass as much territory.

Although the basic premise concerning food distribution and social organization requires further investigation, it appears to be applicable to other primate species. The need to respond to seasonal fluctuation of scattered and clumped resources via group enlargement and/or spreading out of the troop members over a larger foraging area occurs among Cercopithecus mitis (Aldrich-Blake, 1970), Pan troglodytes (Sugiyama, 1973; Reynolds and Reynolds, 1965), and Ateles (Klein and Klein, 1975). Subgroup foraging is also seen among P. h. hamadryas and P. h. anubis in response to harsh conditions and scattered resources (Nagel, 1973; Kummer, 1974). It appears that some diets and habitats are best exploited by a number of communicating individuals spread out over a larger area, and in some cases (e.g. Ateles) exhibiting a fission-fussion system. Struhsaker (1975) indicates that the more "opportunistic" the diet (in the sense of omnivory) the larger the range and the more benefit accured by a spreading out of the group. Klein and Klein (1975) and Gautier-Hion (1973) have extended this view, of increasing foraging efficiency by increasing the number of animals foraging, to the highly insectivorous *Saimiri sciureus* and *Miopithecus talapoin*. These authors report that the large group size and what might be considered "patterned" commotion of these animals serves to flush out insects and make them easier prey.

Thus, one can see that the impact of resource distribution on a species as with the impact of resource density is not a straightforward problem with a straightforward solution. We see that being multimale as opposed to unimale (*C. badius* as compared to *C. guereza*) is one response to resource availability. Daily subgroup foraging as a unimale (*P. h. anubis*) and as a harem system (*P. h. hamadryas*) are alternate adaptations to clumped resources. It appears that the response is influenced by other critical constraints, which may be ecological, phylogenetic and/or physiological. Each species brings its own evolutionary history to an environment. The systemic nature of social organization allows adjustments to be made on many levels, in the various subsystems.

In addition to the density, seasonal fluctuation and spatial distribution of resources, the last variable to be considered here is the influence of predation on social organization. In monkeys protection form predation often takes the form of safety in numbers. The large multimale groups common to savanna and open country species are often viewed as a primary adaptation to predation in these environments (Hall, 1968). It is reasoned that large males can collectively ward off even formidable predators. It is also less likely that an animal in a large group will be taken by surprise. The spatial relations within these large group also lessen the chances that females, especially those with infants, and juveniles will become victims. Arboreal primates, on the other hand, live in trees where the cover provided by dense foliage lessens the likelihood of predation from felids and canids. Therefore, the need for large aggregations with protective males is lessened. Predatory snakes and birds do present a threat to forest-dwelling species but evasive action in the foliage is reasonably successful as an anti-predator device. The existence of solitary males in forest habitats and bachelor bands in open terrestrial environments emphasized the different selective pressures from predation in these two environments.

One must recognize these ecological variables as multidirectional forces of differing magnitudes working to produce a resultant vector; that vector is social organization. In order to understand the interface between ecology and social organization, it must be viewed in evolutionary terms. Thus, any organism is expected to be social only insofar as some benefit is gained by living with conspecifics. In an evolutionary sense the benefit involves reproductive advantages and the enhancement of offspring survival. The efficient exploitation of resources and the successful avoidance of predators are not ends unto themselves, rather they are means to an end. The social organization that functions to provide the most successful environmental exploitation for a particular species may also be limited by another set of constraints imposed by developmental, physiological and reproductive parameters. Thus, another important evolutionary consideration in the understanding of social organization involves the influence of phylogeny.

The Influence of Phylogeny on Social Organization

Ethologists recognize the fact that phylogeny influences social behavior and organization among primates. Concordance between morphological and behavioral phylogeny is not an uncommon phenomenon in the animal kingdom. Although this relation ship has been extensively studied in birds and insects (Moynihan, 1962; Tinbergen, 1969; Delacour and Mayr, 1945), it has been given considerably less attention in primate species. Structural phylogenies based on shared homologous morphological characteristics, especially those that are derived, imply a common evolutionary history. We may postulate that behavioral phylogenies may also represent a common evolutionary history. However, the nature of the relationship between behavior and evolution is complex. As indicated by Mayr (1974), in order to understand this relationship we must investigate the impact of evolution on behavior and the impact of behavior on evolution. Incorporated into evolutionary theory is the concept that certain behavioral changes such as shifts in habitat, diet, etc. may often precede the morphological characters we may currently perceive as adaptive to a particular niche. Such changes bring about new selective pressures, the results of which are new adaptations, i.e., complexes of characters that amplify and extend the initial change (Mayr, 1958, 1974). According to Mayr:

> A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behavior. The adaptations to the new niche, particularly the structural ones, are acquired secondarily. (1963, p. 604)

We may postulate that behavior responds to the process of evolution in a manner similar to that of structural characteristics. Therefore, the radiation of a lineage into a new adaptive zone is not only followed by morphological adaptation but by social adaptations as well. These behavioral changes are equally as important to survival as are morphological ones, and may also become incorporated into the phylogenetic heritage. In practical terms the impact of phylogeny on social organization within any particular group can only be understood if the phylogenetic relationships within the group are clearly determined.

The Old World Cercopithecidae may serve as an example of how the relationship between phylogeny and social structure can be analyzed and understood, if the two prerequisites mentioned above are fulfilled. The family Cercopithecidae is divided into two subfamilies, the Colobinae and Cercopithecinae (Delson, 1975; Simons, 1972; Napier and Napier, 1967). The Cercopithecinae has been further divided into two tribes, the Cercopithecini and the Papionini

(Delson, 1975; Delson and Andrews, 1975). The contrast between these two tribes will serve as an illustration.

The phylogenetic distribution of social organizatoinfor the Cercopithecinae is presented in Table II. The chart indicates that none of the subspecies of the tribe Papionini are unimale. A profile of the tribe indicates that all its member genera live in groups with more than one adult male.

All Papio subspecies, except P. hamadryas hamadryas exhibit the true multimale social structure. They are distributed throughout Africa living in savanna and forest where they are primarily terrestrial. In spite of the variation in group size, manifestations of the dominance hierarchy, and the readiness of animals to change groups, seen in the different environments, the species of Papio remain multimale throughout their range (Rowell, 1972; Ransom and Rowell, 1972).

The previous discussion in the section on Harem Species clearly indicates the inclusion of the P. h. hamadryas and T. gelada harem structures as variants of the multimale pattern. The degree of cooperation and tolerance among males of the harem system indicates to this investigator that the social mechanisms are closer to multimale and age-graded systems than to the unimale system. Thus, all baboons including P. h. hamadryas and T. gelada exhibit a variation of a more-than-one-adult-male structure, living as either generaal multimale or harem.

Table II: Phylogenetic distribution of social organizations among Cerco!ithecinae.

Tribe	Unimale	Harem	Multimale	Age-Graded
CERCOPITHECINI	*Cercopithecus ssp* (except *C. aethiops*) *Erythrocebus patas*		*Cercopithecus aethiops*	*Miopithecus talapoin*
PAPIONINI		*Papio hamadryas hamadryas*	*Papio ssp*	
		Theropithecus gelada	*Macaca ssp*	————————
			Cercocebus	
		? ————————	*Mandrillus ssp*	? ————————

All 12 species of the genus Macaca also live in multimale or age-graded groups. They are distributed throughout Asia and extend into north Africa (Morocco). The success of this genus can be seen in the range of environments they inhabit (e.g., tropical rainforest, temperate forest, savanna and scrub) where they exhibit varying degrees of arboreality and terrestriality. All macaques, as with the baboons, do not exhibit identical social structures; there is variability related to environmental differences. However, as in the case of the baboons, the variability within the genus Macaca is expressed within the context of a multimale group.

Cercocebus and Mandrillus are the only genera of the Papionini to inhabit African tropical rainforest. They have not been studied as extensively as macaques and baboons and thus their behavior is not as clearly delineated. However, we do know that Cercocebus albigena is primarily arboreal while C. torquatus is semi-terrestrial. Both species are reported to live in multimale groups (Chalmers, 1968; Struhsaker, 1969; Jones and Sabatier Pi, 1968). Semi-terrestrial Mandrillus is consistently reported to live in groups with more than one adult male (Gartlan, 1970; Sabatier Pi, 1972; Struhsaker, 1969; Jouventin, 1975) but there is some discrepancy as to whether they are true multimale, age-graded or harem. So again we see that Papionini genera live in groups with more than one adult male.

The behavioral affinities of Papionini species extend beyond demographic consideration. Observations in the field and comparative laboratory investigations have indicated that many aspects of their behavioral repertoires are related and in fact occur within the same contexts (Chalmers, 1970; Rowell, 1966; Chalmers and Rowell, 1971; Rosenblum _et al._, 1964). Social organizations are composed of configurations of social relationships. These relationships are expressed, maintained and regulated by behaviors related to the attraction and repulsion of individuals. The behavioral units shared by members of the Papionini probably reflect a common heritage affecting social relations and consequently social organization.

The general tendency within the Papionini is toward living in open habitat with only a minority of species living in dense forest (e.g., _M. nemestrina_, _Mandrillus_ and _Cercocebus_.) In conjunction there is a strong tendency toward exhibiting some form of multimale social system. These trends are in sharp contrast to the Cercopithecini species whose phylogenetic heritage reflects another direction. All _Cercopithecus_ species (except _C. aethiops_) are arboreal, forest-dwelling and unimale. _C. aethiops_ is the only savanna dweller of this genus and is also the multimale form.

The other noteworthy exception to the unimale tendency of the Cercopithecini is _Miopithecus talapoin_. This species lives in age-graded multimale troops and is exceptional in many traits: its size, its diet (highly insectivorous for a cercopithecoid monkey), and the possession of female sexual swellings (Gautier-Hion, 1971; Hill, 1966; Rowell, 1973). In many respects the talapoin monkey is convergent with Saimiri, both ecologically and socially as will be discussed in greater detail later.

The preceding discussion concerning ecological correlates of social organization established the concordance between terrestrial savanna life and large multimale troops. These groups afford protection from predation and more efficient foraging for scattered resources and omnivorous diets. Thus, the multimale troops of Papio and the open country macaque species (e.g., M. mulatta and M. radiata) are easily understood. The harem group structure of P. h. hamadryas is also easily understood as the coupling of the ecological pressures of savanna life toward multimale groups with very limited resources that necessitate a flexible foraging biomass, i.e., a fission-fusion system in response to prevailing conditions. This system is also noted in P. h. anubis of the Awash region of Ethiopia where these baboons break up into harem-size foraging parties (Nagel, 1973).

E. patas follows the Cercopithecini unimale trend yet lives in an environment that should, according to the present discussion, select for multimale groups. It is admittedly difficult to account for E. patas. Morphologically this species is well adapted to terrestriality and so cannot be a very recent arrival to the savanna. However, it may be possible that competition between it and the multimale Papio precluded selection toward multimale groups of E. patas. Instead of adapting to the savanna as multimale the patas monkey developed male diversionary and patrol behavior. This is, of course, speculative.

It is also difficult to explain the social organizations of the multimale species of the Papionini that do not live in open habitats. As noted by Struhsaker (1969) the multimale groups of Cercocebus and Mandrillus can not be accounted for on ecological grounds since they do not differ significantly enough from their Cercopithecus neighbors. An influence of phylogeny may also occur in those macaques, such as the pig-tailed monkey, that live in dense tropical rainforest since they like other Papionini have a multimale structure. Attributing phylogeny with a principal role in the determination of social organization is not a negation of environmental influence, but rather invokes ecological causation on another level.

The evolutionary history of the Papionini includes semi-terrestrial adaptations as far back as the Miocene (Delson, 1975; Simons, 1972). According to Delson the two morphs of the fossil Victoriapithecus indicate a middle Miocene split between the Colobinae and the Cercopithecinae. The cercopithecine evidence indicates the beginnings of semi-terrestrial adaptations. Perhaps in the late Miocene (10-12 million years ago) there was another split involving the cercopithecines. This second split resulted in the tribes Papionini and Cercopithecini (Delson, 1975). It appears that the Papionini continued to exploit the terrestrial adaptations whereas the Cercopithecini returned to the forest and arboreality. Papionini fossils from the Late Miocene, Pliocene and Pleistocene, including specimens referred to _Macaca_, _Papio_, and _Theropithecus_ document the continuing evolution of this group as terrestrial (Delson, 1975; Simons, 1972). The similar social organizations of species of the Papionini may be the result of this long evolutionary history and radiation in terrestrial environments resulting in specific demands and constraints on their social structure.

The Cercopithecini do not have a phylogenetic history involving millions of years of terrestrial adaptation. Their radiation occurred in the forest where selective pressures were different from those in the savanna and these pressures were probably not in the direction of multi-male groups. Consequently, _Cercopithecus_ monkeys are unimale. The arguments put forth by Gartlan (1958) and Crook _et al._ (1976) suggest that the association of males with females must be considered in terms of functional roles filled by the males _vis a vis_ ecological demands and the long range benefit provided to the offspring. It would seem that generally speaking the niches within the African forest occupied by _Cercopithecus_ do not select for multimale systems. The only multimale species of this genus is the already mentioned _C. aethiops_ whose savanna habitat selects for multimale groups.

The comparison of these two tribes indicates that the social adaptation of any given species may be significantly influenced by its phylogeny. As Kummer has suggested:

> Cultural developments, like other modifications, are restricted by the phylogenetic heritage of the species... (Kummer, 1971, p. 90).

It does seem that within any group there exists the possibility that part or all of their radiation involved certain critical pressures that exercised as much long range influence on their behavior as on their morphology.

Phylogenetic relationships imply structural similarities. Phylogenies are inferred from presumed shared derived homologous morphological characteristics. In turn, these phylogenetic structural similarities are based upon genetic affinities resulting from a common evolutionary history. The preceding discussion of Cercopithecinae supports the claim of many authors that phylogeny influences the expression of social organization. Implicit in the acknowledgment of a connection between phylogeny and social structure are several theoretical concepts concerning behavior: (1) that behavior evolves, (2) that if behavior evolves, it is subject to evolutionary principles, and (3) if the shared behavioral and organizational similarities are due to phylogenetic causes, there must be some genetic base, i.e., behavioral-genetic affinities resulting from a common evolutionary history.

Evolutionary theory as currently understood does not conceive of alternate mechanisms of 'descent with modification' *vis à vis* behavior and therefore in the words of Mayr:

> If the evolution of behavior proceeds like the evolution of structural or molecular characters, then, according to the Darwinian interpretation, it must have two characteristics. First, in order to be able to respond to selection pressures, such behavior must at least in part have a genetic basis, and secondly, the genetic basis must be somewhat variable, that is, it must be able to supply the material on which natural selection can act. (Mayr, 1974, p. 653.)

Genetics and Behavior

Mayr's logic is persuasive. It is difficult to imagine that the rules of evolution have been suspended for behavior; and indeed the investigation of invertebrate organisms has revealed a great deal of genetic substrate to behavior (Hirsch, 1967). However, the genetic constituents of cricket songs and the cell cleaning behavior of bees are of a different order of magnitude from social interaction among primates. Again, we may turn to Mayr (1974) to help clarify the issue. It may be said that there are two types of genetic programs, open and closed. According to Mayr:

> A genetic program which does not allow appreciable modifications during the process of translation into the phenotype I call a *closed program* - closed because nothing can be inserted in it through experience. Such closed programs are widespread among the so-called lower animals. A genetic program which allows for additional input during the lifespan of its owner I call an *open program.* (Mayr, 1974, p. 651.)

The reality of closed and open genetic programs is not as dichotomous as the terminology implies. No programs are totally open or totally closed. As indicated by Mayr (1974), "an open program is by no means a *tabula rasa.*" The degree to which a program is open or closed depends on the selective pressures in the evolutionary history of the organism. In order for an open program to have a selective advantage, the organism possessing the trait must have enough cortical area to incorporate and store learned information and a long enough life span to obtain the information and utilize it. Particularly important is the length of the period of parental care. The longer the time spent at 'the mother's knee', the more information that can be exchanged.

The anthropoid primates possess several characteristics which are prerequisites for an open genetic program, including a relatively long life span, an extended infancy and juvenile period and an expanded neocortical area. The preceding discussion on phylogeny and Mayr's view of behavioral evolution indicate that the program can not be totally open and that there must be some genetic substrate to behavior. For example, an infant monkey's recognition of its own species has been demonstrated to be an innate behavior, present even without the benefit of a social environment (Sackett, 1973). However, it is difficult to imagine the mechanisms by which the more complex behavior patterns of primates could be encoded.

It is useful to remember that the encoded behavior pattern is never a direct product of the chemistry of the genome. In between the genome and the manifestation of the behavior are many processes including RNA transcription, protein synthesis and translation by the nervous system.

Thus, there is room for the experiential information gained by the organism to be inserted into the nervous system's translation of the genetic program. Innate behaviors are therefore modifiable and amplifiable via socialization, and therefore no longer 'innate'. Thus we have a semantic rather than a biological problem.

Hormones and Behavior

It has long been recognized that one step in the translation process of a behavioral-genetic program resides in the influence hormones exert on behavior. Recent studies concerning the mechanism of hormone action have indicated that steroids act by directly influencing gene expression (Turner, 1976; Thompson and Limppman, 1974). The action of steroids upon the genome has been shown to involve mRNA transcription and the availability of certain genes for transcription. Although the exact mechanisms of steroid action are still being delineated the influence of steroid hormones on behavior has been demonstrated by many investigations of primate behavior (e.g., Goy and Phoenix, 1972; Rose *et al.*, 1974).

The relationship between hormones and behavior and the manner in which hormones exert an influence on behavior can be seen to be a two dimensional process. The action of hormones on the brain in fetal or neonatal life is inductive and in adult life is either excitatory or inhibitory. As indicated by Beach:

> Hormones are capable of influencing behavior in two distinctly different ways. Effects belonging in one category are usually referred to as 'organizational' or 'developmental'. These effects characteristically are exerted during prenatal life or very shortly after birth. A more familiar type of effect is that known as 'activational' or 'concurrent'. Such effects take place more or less at the time the behavior is manifested. (Beach, 1974, p. 7.)

Beach further clarifies the relationship between hormones and behavior by indicating the manner in which behavior can be affected:

> One can think of at least three ways in which a hormone could influence the occurrence of a given type of behavior. (1) It could alter effector structures, thus increasing or decreasing the ability to perform certain responses. (2) It could control sensory or perceptual mechanisms in such a way as to modify the reception of environmental stimuli. (3) It could induce changes in central neural mechanisms responsible for interpretation of incoming information and/or organization of overt patterns of response. (Beach, 1974, p. 7.)

Male and female mammals do not possess the same behavior patterns. There are differences not only in adult life but also very early in the ontogeny of the individual. It is difficult to imagine that the distinctive behavior patterns of males and females are the result of mutually exclusive genetic or socialization processes. Rather, the two must go hand in hand, with certain predispositions created by the genes being subsequently modified by social forces. The conceptual framework provided by Beach addresses itself directly to the problem of understanding behavioral differences between the sexes as partially a ramification of the hormonal differences between the sexes.

The sexual differentiation of a mammalian fetus is a hormonally-controlled process. The androgen produced by the fetal testes not only causes the development of male genitalia from a neuter anlagen but also has an organizing effect on the differentiation of neural tissue (Beach, 1974; Resko, 1971). The importance of fetal androgen to the subsequent appearance of male behavior in the adult has been demonstrated in rodents and in the rhesus monkey. Normative observations on isolate reared infant rhesus monkeys indicates that innate differences between the sexes exist (Rosenblum, 1961). In addition, experiments involving the manipulation of the hormonal environment of the fetus, have indicated that behavior in later life can be altered (Goy, 1968; Ward, 1972).

In 1961, Rosenblum demonstrated that the behaviors of surrogate-reared male and female rhesus monkey infants were significantly different, especially regarding play patterns. These results were corroborated by Goy (1968) who found that the frequency of threat, play initiation, rough and tumble play and chase play was significantly higher for males than females. In order to determine if the prenatal androgen of the males was the significant factor, pregnant rhesus females were injected with testosterone during the critical differentiation period, thereby masculinizing the female fetuses (Goy, 1968; Goy and Phoenix, 1972). The behavior of the masculinized females was significantly affected by the exposure to androgen. Their play patterns, play scores and mounting frequencies were significantly shifted in the male direction.

The influence of testosterone on behavior has been further indicated by Ward (1972). Cyproterone acetate is an anti-androgen. When it is injected into pregnant rats it blocks the action of testosterone on male pups. These pups later exhibit significant feminization of their adult sexual behavior patterns. In addition to influencing play and sexual behavior, testosterone in adults has also been implicated in the mediation of aggression (Bernstein *et al.*, 1974; Rose *et al.*, 1974). These data have indicated that the hormone-behavior relationship can be a reciprocal one: the expression of behavior may be influenced by the endogenous hormone titers and conversely, certain behaviors can influence the circulating levels of hormones.

Thus, there is a great deal of data indicating that hormones influence behavior, both prenatally and postnatally. These influences may be one of the mechanisms for providing complex behavior patterns with a genetic substrate that is open to socializing forces. However, in order to understand how hormones, by affecting the behavior of an individual, can affect social organization we must understand the relationship of the individual to the social organization.

In order to understand social organization, one must resolve the structure into its constituent parts (Hinde and Stevenson-Hinde, 1976). Social structure is a system comprised of relationships between individuals. In fact, members of a social group participate in relationships and not in the social structure per se. These relationships connote various degrees of attraction and avoidance and are the accumulation of numerous interactions or lack of interactions over time. The behavioral repertoire of the individual determines the interaction. Thus, hormones that affect the behavior of the individual also affect the interactions of the individual with conspecifics. The interactions affect the relationships and thus the social structure is also affected. Therefore, it is critical to view social structure in terms of very discrete behavioral units that if altered also alter the social organization.

An example of the relationship between behavioral units and social organization may be seen in the work of Nagel (1973) on hybrid baboons. A hybrid male from a *P. h. anubis* and *P. h. hamadryas* mating does not appear to have the complete behavioral repertoire of a pure-bred hamadryas male even though living in a hamadryas troop. The female herding techniques of the hybrid males are incomplete or insufficient and therefore the relationship between the male and his females is considerably different from the relationship between a full hamadryas male and his females. This deficit in the behavioral repertoire influences the hybrid male's relationships with his females and causes the harem to be unstable. In this example, we can see how an altered behavioral unit can affect more than the individual possessing it, influencing the social structure via altering interactions which affect relationships. The research to be presented on _Saimiri_ was undertaken to investigate these interrelationships.

It is for this reason that the research on _Saimiri_ was undertaken. The research to be presented represents an investigation of hormonal influence on the behavior of squirrel monkeys and of how that influence affects _Saimiri_ social organization. In the following section _Saimiri_ social organization will be discussed, especially in relation to its reproductive cycle.

CHAPTER THREE

THE SQUIRREL MONKEY

The Squirrel Monkey

Taxonomy and Ecology

Saimiri sciureus, commonly referred to as the squirrel monkey, is a haplorhine primate of the family Cebidae (Napier and Napier, 1967). The squirrel monkey is the most widely distributed diurnal New World primate, spanning the South American continent from Peru to the Guyanas and ranging north through Colombia into the Central American countries, Panama and Costa Rica (Thorington, 1968; Baldwin and Baldwin, 1971; Napier and Napier, 1967). Napier and Napier (1967) classify Saimiri into two species, the South American S. sciureus and the Central American S. oerstedi. However, recent investigations have indicated that probably only one species but several subspecies of Saimiri exist. In this paper only one species is recognized. Pending definitive classification geographical origin will have to substitute for subspecific assignments.

The pelage of Saimiri varies geographically and specimens from Peru, Colombia, Brazil, Bolivia and Guyana are easily distinguishable by their markings, especially on the face, head and forearms. All are a mixture of black, white, and yellow-orange, often giving the animal an olive hue. Central American _Saimiri_ is known as the red-backed squirrel monkey and its bright orange coloring is quite distinctive.

As indicated above, recent karyological data suggest that the two species classification of _Saimiri_ is in need of revision (Jones _et al._, 1973, 1975). Examination of specimens from the major exporting regions of Iquitos, Peru; Leticia, Colombia; and Georgetown, Guyana, as well as specimens from Costa Rica and Panama, reveals three distinct karyotypes. All monkeys possess a diploid number of 44 chromosomes but vary in the number of submetacentric chromosomes. Animals from Costa Rica, Panama, Bolivia, and Peru comprise one karyological type containing 22 submetacentric chromosomes. _Saimiri_ from Leticia possess 20 submetacentrics and those from Guyana have 18. Jones _et al._ (1973) examined the hybrid offspring of parents from Iquitos and Leticia and found the number of submetacentrics to be 21. Baldwin and Baldwin (1976) and Jones _et al._ (1973, 1975) favor the recognition of geographically distinct subspecies of the _sciureus_ species as opposed to recognition of _oerstedi_ on the specific level.

Personal observations indicate that _Saimiri_ from Leticia and Iquitos will inter-breed in captivity and readily interact in mixed social groups. Although socially compatible they differ in temperament. Brazilian squirrel monkeys are considerably more vocal and hyperactive than Peruvian monkeys in captivity.

Saimiri are relatively small-bodied for diurnal primates. The body weight of normal adult males in the laboratory ranges between 750 to 1400 g and adult female weights range from 600 to 900 g. Within this range Brazilian male and female Saimiri and Bolivian squirrel monkey males tend to be somewhat larger than their counterparts from other areas, which again reflects the subspecific variation.

Saimiri, like all South American primates, is arboreal, although several farmers in the Llanos of Colombia claim that the monkeys periodically descend to the ground to raid maize fields (personal communication, 1975). Baldwin and Baldwin (1972) reported that during the dry season in Panama when food was scarce, Saimiri would occasionally forage on the ground. However, these forays were usually less than a minute long and the monkeys always returned to the trees to eat the food they had obtained. Squirrel monkeys are extremely agile. Their basic mode of locomotion is quadrupedal running and leaping (personal observations; Napier and Napier, 1967; Rose, 1973).

Their extensive range includes varied habitats and they can be found in tropical rainforest, inundated forest, gallery forest and on forest edges (Thorington, 1968; Baldwin and Baldwin, 1972; Napier and Napier, 1967). Saimiri generally remain in the middle and lower canopy but have also been observed in the emergents. They are usually found sympatric with Cebus, Alouatta and Aotus, and less frequently with Callicebus (Thorington, 1968). The diet of the squirrel monkey consists primarily of insects and fruit but also includes flowers, buds, and shoots in smaller quantities (Fooden, 1964; Thorington, 1968; Baldwin and Baldwin, 1971). The water requirements of Saimiri are high, and captive animals can easily succomb to dehydration. This is especially true for pregnant females (Clewe, 1969). During the last trimester of pregnancy and during early lactation, daily water consumption is often more than 50% of the animal's total body weight. Presumably in the wild this requirement is met via consumption of substances containing moisture. Fruits and even insects in large quantities can provide considerable moisture.

Squirrel Monkey Social Organization

Saimiri live in age-graded multimale groups which as previously described are sexually segregated. Troop size varies from one habitat to another (Baldwin and Baldwin, 1971). Troops which live in undisturbed Amazonian forest tend to be large containing up to 300 individuals. In contrast, troops which live in drier areas and in areas which have been disturbed by human habitation, e.g., Llanos region of Colombia, tend to be somewhat smaller, ranging from 10-35 animals. Older reports on South American wildlife indicate that large Saimiri troops were common as recently as thirty years ago (da Cruz Lima, 1945). The smaller troops appear to be highly correlated with large scale forest destruction and human incursion upon the forested areas. The destruction of primate habitats in South America has occurred at an extremely rapid pace in the last thirty years and small *Saimiri* troops may be a recent development. The large size (ca. 100 or more) of Amazonian troops is unusual for tropical rainforest primates. Only the 50-60 member groups of *Miopithecus talapoin* rival *Saimiri* in troop size (Gautier-Hion, 1971), as do the 40-80 member troops of *Colobus badius* (Clutton-Brock 1975).

Saimiri troops are organized into subgroups comprising animals of the same age and sex (Baldwin, 1968, 1971). Social interactions are primarily within age/sex subgroups rather than between them. The term *sexual segregation* used to describe *Saimiri* social organization reflects the delimited nature of the interactions between males and females. The only other multimale species which shows this social pattern in that there is a minimal amount of affiliative behavior between adult males and females is *Miopithecus talapoin*.

Saimiri females appear to be the social core of the troop (Baldwin, 1968, 1971). They are more socially initiative than the males and also dominate social interactions between the sexes. Female domination is a collective endeavor, manifest in cooperative displacement and aggression against transgressing males. The matriarchal nature of the society is similar to that seen in talapoins. *Lemur catta* females also form a matriarchal social core but their organization is not as segregated as that of Saimiri and talapoins. Observations in the laboratory and in the semi-natural environment of Monkey Jungle, Miami, reveal that most social activity occurs within or near the female core (Baldwin, 1968, 1971; Coe and Rosenblum, 1974). The males appear to be less social than the females, and they remain more or less peripheral to the troop, especially during the non-mating season. Young infants less than one year of age are the primary exception to the general pattern of interacting within rather than across age/sex subgroups. In fact, infants are a strong attractant for young and old females without infants of their own. Saimiri females will develop alliances with mothers and also 'aunting' relationships with the mothers' offspring ("allomothering" Hardy, 1976). The only other exception to the pattern of interacting within age classes is the possible guardianship role young adult males may have in relation to juveniles of one to two years of age. Unpublished studies in the Llanos and Amazonas regions of Colombia indicate that a young adult male may travel with a group of juveniles and wait at difficult and dangerous crossings until all the juveniles have passed safely (personal observation; Coe, personal communication). Personal observation of a large captive group in the Primate Behavior Laboratory (Downstate Medical Center, New York) also indicates that young males may maintain a guardianship role towards juveniles of both sexes. This relationship is similar to the one reported for talapoin males (Rowell, 1973).

As indicated by the preceding descriptions, the primary divisions an observer of a *Saimiri* troop would become aware of include: (1) a group of mothers and infants, (2) an associated group of male and female juveniles, (4) a group of sub-adult males, and (5) the relatively more isolated adult males. The preceding discussion also indicates that it is the strong mutual avoidance between adult males and females that constitutes the core of sexual segregation. The preference of adult squirrel monkeys for interaction with members of their own sex has been shown by many investigators in acute partner preference tests and in laboratory social groups (Fairbanks, 1974; Mason, 1974, 1975; Candland *et al.*, 1973). The ontogeny of segregation has been delineated by Coe and Rosenblum (1974). The latter authors observed that juvenile *Saimiri* living in a heterosexual social group do not preferentially interact with their own sex. Male and female subadults living without adults also freely interact. However, when the subadults are introduced into a segregated adult group, they too segregate. The subadult females are attracted to and are ultimately admitted to the adult female group. The young males tend to be peripheralized although they also move towards the adult males. Juvenile squirrel monkeys do not respond in the same manner. Contact with an adult group does not lead to segregation. Rather they remain as a separate heterosexual juvenile group.

These data were confirmed in another large multi-age group containing mothers and infants, juveniles, subadults, adult males and females. (Bromley, unpublished data). Again, young adult females joined the adult female group without infants. This group maintained very close contact with the adult females with infants. The subadult males remained peripheral to the adult females and males who would not tolerate their presence. The juveniles remained close to the subadult males. Saimiri males, like many other primate males, appear to have a more prolonged period of social maturation.

The indications are that in order for sex segregation to emerge: (1) an adult social structure must be present as a necessary socializing force and (2) that in order to respond to socialization, a certain maturational level must be attained (i.e., the animals must be post-pubertal). This implies that gonadal hormones play a role in the emergence and maintenance of sexual segregation.

The effect of gonadal hormones on the behavior and social organization of Saimiri can also be seen if one examines the changes that occur during the annual breeding season. The mating season of squirrel monkeys, as well as of talapoin monkeys, rhesus monkeys and ringtailed lemurs, is accompanied by behavioral changes (Baldwin, 1970; Jolly, 1966; Rowell and Dixson, 1975; Rose et al., 1974). In both squirrel monkeys and rhesus monkeys these behavior changes have been shown to correlate with changes in the circulating levels of endogenous gonadal hormones.

Squirrel Monkey Reproduction

Squirrel monkeys exhibit an annual reproductive cycle. In the wild, mating occurs for 2-3 months during the dry season and births occur for 2-3 months at the beginning of the rainy season. Squirrel monkeys maintain their annual cycle even under captive conditions although seasonality in the laboratory is less demarcated than in a semi-natural environment (Rosenblum, 1972). A seminatural colony composed of animals imported from Iquitos, Peru to Monkey Jungle in Miami altered their mating and birth seasons a few months at a time over a three year period until the cycle corresponded to the new climatic conditions (Dumond, 1968). Both males and females exhibit physiological and behavioral correlates of the respective reproductive periods.

During the non-mating season, the males are typically described as docile and socially inactive (Baldwin, 1968). They maintain a dominance hierarchy which can be discerned by the direction of the genital display (Ploog *et al.*, 1963). The dominant male is never displayed to by subordinates whereas the middle-ranked males may display back and forth to each other. Aggression is very low during the non-mating season and hierarchical positions are generally not contested. During the mating period, however, the males' demeanor is altered considerably. Squabbles between males are frequent; the occurrence of the genital displays increases and there is a great deal of agitation among the males. In contrast to their behavior during the non-mating season, males approach and pursue females and exhibit long bouts of courtship behavior. The courtship pattern involves a series of chases, species-specific darting behaviors and mounts (Latta _et_ _al._, 1967). The male jumps back and forth in front of the female; if she is receptive she will perform a squat-present, deflecting her tail and orienting her rump towards the male. The male will pounce on her and mount; 10-25 separate mounts typically occur before ejaculation but ejaculation may occasionally occur on a single mount. The courting male and female pair may become the object of a great deal of aggression and interference from other group members, and as a consequence, they may move to the periphery of the troop during the mounting series.

The behavioral changes exhibited by the females during this period include increased tolerance of male approaches and an increase in their own frequency of approaches to males. As consequence of the increased agitation and increased male-female interaction, the social organization during the mating period is somewhat altered. Rowell and Dixson (1975) report very similar findings for _Miopithecus_ _talapoin_. Jolly (1966) reports that male _Lemur_ _catta_ become extremely agitated during their very short breeding season, often changing groups and engaging in scent-marking bouts, called 'stink fights'. Male rhesus monkeys are also reported to undergo behavioral changes during the mating season, including an increase in aggression and inter-troop movement (Wilson and Boelkins, 1970).

In addition to the behavioral changes described above, the males and females undergo an annual physiological rhythm. Female Saimiri are seasonally polyestrous (Wolf et al., 1975). About 5-6 months after giving birth, a female squirrel monkey will resume estrous cycles (Coe and Rosenblum, submitted). Saimiri females exhibit a very short cycle, typically reported to be 7-8 days in length (Rosenblum, 1968; Wolf et al., 1975). However, their cycle has been reported to vary, increasing to 10-12 days in length (Hutchinson, 1970). As indicated by Gould et al. (1973) and Hutchinson (1970) the length of the cycle is strongly affected by the environment in which the females live and the conflicting reports do not necessarily represent mistakes by the respective investigators. Rather, they reflect the differential response by the females to the living conditions in the different environments. In comparison to other primates, any of the reported cycle lengths are relatively short. However, the cycle length for Cebus, which is phylogenetically close to Saimiri, ranges between 16-20 days, also short in comparison to other primates (Butler, 1974; Hafez, 1971). The reported lengths for most Old World primate estrous cycles are usually between 25-45 days dependings upon the species. Additional information concerning the reproductive physiology of other Ceboidea is necessary in order to evaluate whether Cebus and

Saimiri are distinctive or typical of a trend in New World monkeys. For example, Ateles has a cycle length of 24-27 days which is on the lower end of the range for Old World monkeys (Napier and Napier, 1967).

Female Saimiri who do not become impreganted during the mating season may become acyclic during the pregnancy and lactation phases of the other females (Coe and Rosenblum, submitted). This seasonality is also reflected in the circulating levels of estrogen. According to Mendoza and Levine (personal communication) intact Guyanese females living in a social group with vasectomized males exhibit an annual hormonal rhythm. The mean circulating level of estrogen in the non-breeding season was 48 pg/ml and in the breeding season rose to 361 pg/ml. The existence of an annual hormonal cycle was further indicated by O'Connor and Wolf (1971). They found seasonal fluctuations in the levels of plasma progestins in Saimiri females. Females sampled in September had a mean of 27 ng/ml whereas the same females sampled in January had a mean of 189 ng/ml. Although no causal relationships can be drawn from these data, it is evident that an annual hormonal cycle parallels the annual behavioral changes in Saimiri females.

The squirrel monkey male also exhibits an annual physiological cycle. During the breeding season sexual dimorphism between the male and female Saimiri is accentuated by a phenomenon known as the "fatting response" (Dumond and

Hutchinson, 1967). At this time the males are 100-300 g heavier than during the non-breeding season, due to additional weight about the head, neck and shoulders. The weight gain actually takes a slow course, with small increments over several months until a peak is reached in the mating season. After the peak there is a slow decline to a low weight point in the birth season, the whole fatting cycle represents six months of increase and 6 months of decrease. The testes also undergo a cyclic volume change reaching maximal volume in the mating season (Coe and Rosenblum, in press). This probably reflects cyclic changes in the seminiferous tubules since Dumond and Hutchinson (1967) have reported that Saimiri males are not spermatogenic throughout the year. The seminiferous tubules regress during the non-mating season. Again, the regression of the tubules is a slow decline rather than an on/off phenomenon. Testicular biopsies indicate that in the regressed state the seminiferous epitheleum is greatly reduced and there is little evidence of mitotic activity. This regression is essentially the same as that described for rhesus moneky males (Conway and Sae, 1965). During the non-mating season only spermatogonia are visible along the basement membrane and the lument is greatly enlarged.

In addition to the annual cycles of body weight, testicular volume and spermatogenesis, there is an annual cycle of circulating testosterone. Mendoza and Levine (personal communication) indicate that the mean circulating testosterone level in Guyanese males during the non-mating season is 9 ng/ml. The level rises to a mean of 44 ng/ml during the mating period. The Leydig cells do not appear to undergo any seasonal regression (Belt and Cavazos, 1971). There appears to be no information available concerning cyclic changes on the Sertoli cells.

The relationships among the fatting phenomenon, the annual testosterone fluctuations and the spermatogenic cycle are still not clearly understood. Only correlations, as opposed to causal relationships appear to exist. Nadler and Rosenblum (1972) reported that testosterone injections to castrated males resulted in a prolonged weight increase. However, Mendoza and Levine indicated that the weight and testosterone cycles may be somewhat dissociated. Furthermore, males are capable of siring offspring in the middle range of the annual weight cycle (Coe and Rosenblum, in press).

Although testosterone appears to play a significant role in fatting, the increase in testosterone is probably not the primary cause of fatting in Saimiri males. Testosterone may synergize with or have a permissive action with another hormone or hormones, and together these hormones may be responsible for fatting. Prolactin has been implicated in restoring weight and spermatogenesis to the regressed testes of hamsters. Polactin also increased testosterone levels in the hamster (Bartke, 1975; Reiter, 1975). Further research on hormonal interactions in the squirrel monkey may also indicate a relationship between testosterone and prolactin underlying the annual cycle.

As indicated in the preceding discussion, the annual cycle in Saimiri is a series of behavioral and reproductive phases. Each of these behaviorally distinct phases is correlated with a distinct phase in the yearly hormonal cycle. The correlation of these behavioral changes with changes in hormone production leads one to believe that a causal rather than coincidental relationship exists.

It has been established thus far that in order for hormones to affect the social structure they must influence the behavior of the individual which in turn affects interaction patterns and finally relationships. Therefore, we would expect that the hormonal status of an individual might affect, for example, partner preferences, as indicated by Mason's work on pairs of squirrel monkeys (Mason, 1974, 1975). Alvarez (1969) indicated that gonadectomy did affect the social pattern of sex segregation in the squirrel monkey. However, since all of his males and females were gonadectomized it is difficult to resolve the effect into its components; specifically to understand the effect on female behavior separately from the effect on male behavior. The mechanisms by which hormones influence Saimiri social organization must involve specific and separate effects on the males and females.

Therefore, in order to delineate the separate male and female behavior patterns that might be affected by hormones and thereby affect the social organization, the following research was undertaken. It was hoped that this research would not only elucidate the influence that hormones exert on the behavior and social structure of _Saimiri_ but also indicate a possible mechanism by which complex social organizations can be partially genetically encoded and hence subject to selective pressures. The results of this research would, therefore, aid in the understanding of the evolution of behavior in primate.

CHAPTER IV

METHODS

Subjects

The subjects of this study were 28 wild-born squirrel monkeys (*Saimiri sciureus*) obtained from Iquitos, Peru. The monkeys were imported as adults as indicated by their stature, weight, and dental condition upon arrival in the laboratory. All subjects had been members of the colony (Primate Behavior Laboratory, Downstate Medical Center, New York) for a minimum of five years prior to this research. During their tenure in the laboratory, they were housed in heterosexual social groups where food and water were available *ad libitum*.

Prior to inclusion in one of the four study groups (see Table II), the subjects were screened for certain physical and social criteria. Each group consisted of 12 animals, 6 males and 6 females. Some subjects were observed in more than one experimental condition (see Table III). Each of the four groups consisted of two subgroups of 3 males and 3 females who knew each other prior to inclusion in this study. The laboratory history of each animal is available in Appendix A. A record of each subject's health and weight is presented; the birth records of the intact females are also included. The subjects' weight remained relatively stable during the

Table III: Designation and composition of the experimental groups.

Designation	Subject Composition				Length of Observation
1	six ovariectomized females		six intact males		six weeks
	204	145	234	285	March - April
	205	169	235	303	
	206	415	268	329	
1H	six ovariectomized females receiving estrogen		six intact males		six weeks
	204	145	234	285	June - July
	205	169	235	303	
	206	415	268	329	
2	six intact females		six castrated males		six weeks
	146	218	24	416	March - April
	148	279	34	421	
	195	233	98	57 deceased	
3	six ovariectomized females		six castrated males		six weeks
	145	279	24	416	November - December
	195	348	93	421	
	206	415	173	438	

observations and season fluctuations were not evident.

The castrated males of Groups 2 and 3 and the ovariectomized females of Group 1 had been gonadectomized post-puberally five years prior to this study. Three of the ovariectomized females in Group 3 had been gonadectomized post-puberally six weeks prior to the beginning of observations.

Housing

The four experimental groups observed in this study were quartered in one of two identical living areas. Each area consisted of two pens (137cm x 91cm x 230 cm) connected by a tunnel 18cm in diameter (see Figure 1). Each pen had four shelves constructed of aluminum pipe evenly-spaced at 46cm intervals from the floor to the ceiling. A 22cm deep partition was placed in each pen 46cm from the wall opposite the tunnel. This partition afforded the monkeys an easily negotiable visual block. The front wall of both pens contained a 61cm x 107cm one-way glass window which allowed for undetected observation while permitting an unobstructed view of the entire pen.

Each pen was equipped with two automatic watering spouts which provided water ad libitum. The subjects' diet consisted of Purina New World Monkey crackers available in dry form all day in both pens and an afternoon ration of fruit and crackers moistened with milk and vitamins. Illumination and temperature within the pens were constant throughout the study, providing twelve hours of light and twelve hours of

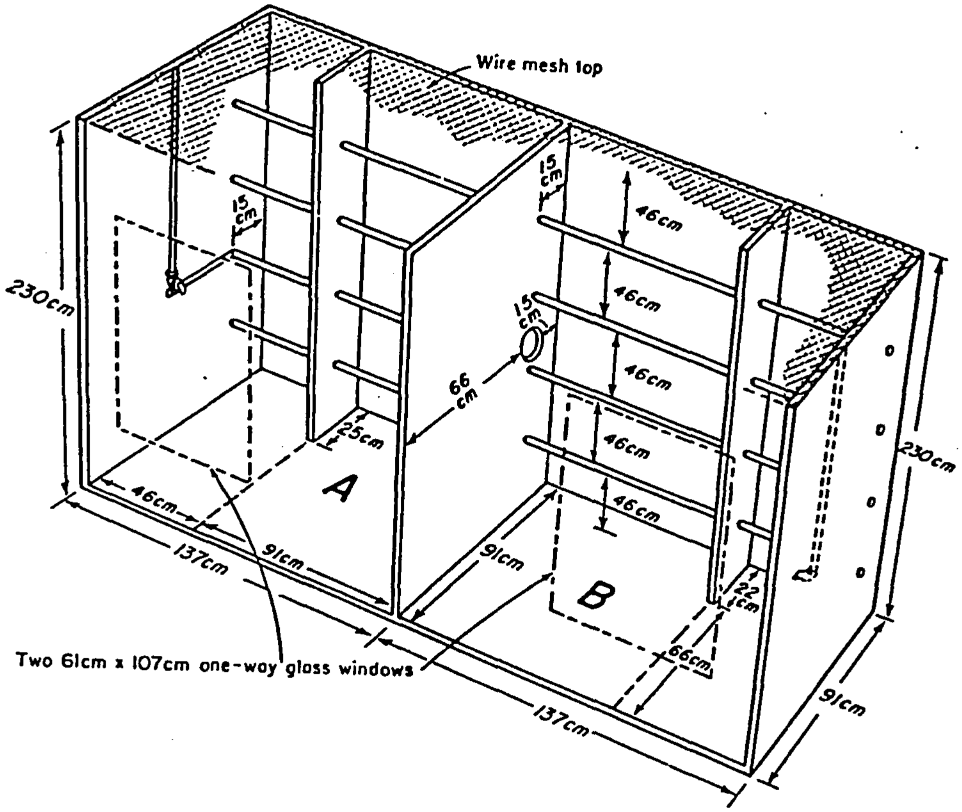


Figure 1: Diagram of the living area for all groups in this study.

darkness in a 23°C environment.

Experimental Procedures

Each of the experimental groups was formed in an identical manner. The selected members were simultaneously introduced into the test pens. Preliminary notes were taken on the initial interactions and the group was informally observed for one week. Data collection began the following week which allowed the monkeys time to acclimate to the new pens and the new group members. Each group was observed for six weeks. Groups 1 and 2 were observed simultaneously during the months of March and April. Group 1H was observed in June and July, following a hormone induction period. Group 3 was observed the following November and December.

Group 1 consisted of 6 ovariectomized females and 6 intact males. Following the six weeks of observation each female received an estrogen replacement regime of 1mg depo-estradiol (Upjohn) injected intramuscularly once every two weeks. Once this hormone regime began this group was designated Group 1H.

Observations did not resume on Group 1H until two injections had been administered in order to allow for the central nervous system and peripheral target tissues to be well under the estrogenic influence. After one month, one week following the appearance of estrous-like smears, observations began and lasted another six weeks. During this time the females received three more injections.

Group 2 consisted of 6 castrated males and 6 intact females. One of the males, number 57, developed a pulmonary infection and died one and a half weeks after observations began. In order not to disrupt the group, he was not replaced. In addition to the familiarity criterion described previously for selecting subjects, the intact females of this group were screened for cyclic ovarian activity. At the time of selection, vaginal smears revealed that all females were undergoing estrous cycles.

Groups 3 consisted of 6 castrated males and 6 ovariectomized females. The subjects of this group were 3 ovariectomized females previously observed in Group 1 and 3 castrated males with whom they were familiar. The other subjects were 3 ovariectomized females, gonadectomized six weeks prior to the observations and 3 castrated males from Group 2 with whom they were familiar.

In order to obtain normative baseline data a control group of 6 intact males and 6 intact females was established. Unlike the experimental groups extreme agitation and fighting among the males followed group formation. We do not know why this group responded to formation with more agitation than the others. Two of the 6 males were severely wounded and would probably have died if not removed from the group. Therefore the group was disbanded within the 24 hours following formation. Despite a colony of 150 *Saimiri*, it was impossible to establish another group that met all the critical criteria of the experimental groups (e.g. familiarity, years spent in the laboratory etc.). A prior study on intact Saimiri (Coe and Rosenblum, 1974) utilized the same techniques and environment as this study and therefore will be considered in the discussion as representative of normative baseline data.

Methods of Data Collection

The data collected in this study fall into one of three categories: (1) observations of social behavior utilizing a 30-second time sampling technique; (2) observations of the spatial arrangement and aggregation of the animals, utilizing a pen-mapping technique five times per day and (3) analysis of the estrous cycles of the females by examination of vaginal smears three-four times per week.

(1) Observations of Social Behavior

Observations were carried out four mornings a week between 9:30 and 11:30 a.m. In order to obtain valid frequency counts and to not bias the observations in favor of attention-getting behaviors, the subjects were observed one at a time focal animal technique in a predetermined random order (Altmann, 1974). Each subject was observed during each observation period for three minutes divided into six thirty-second intervals. The beginning of an interval was signified by the light of an automatic timer, at which time the observer recorded the subject's location. The light was not visible to the monkeys.

The behavior of the focal animal was then recorded until the next light flash. This sequential sampling was continued for six contiguous intervals. A sample data sheet is provided in Appendix B. The behaviors recorded are defined below:

Behaviors involving body contact

1. Contact: body contact between two or more animals without huddling or holding.
2. Huddle: body contact between two or more animals in a stereotyped curled-over resting posture, involving the curling of the tail over the back and shoulder and the head resting on the chest.
3. Social exploration (sosex): the inspection of an animal's body or genitalia by another animal, either by olfaction or manual manipulation.
4. Manual aggression: hostile pushing, pulling or wrestling between two or more animals.

Non-Contact Interactions

1. Proximity: two or more animals within arm's reach of one another without touching.
2. Approach: the movement of one animal toward another animal; recorded only if contact or proximity is attained.
3. Displace: the movement of one animal toward another animal causing the latter to leave contact or proximity.
4. Display: a stereotyped *Saimiri* behavior involving the abduction of one leg and the orientation of the displayer's genitalia toward the receiver's face; in

males the penis is erect and in females the clitoris exhibits a degree of erection (Hopf *et al.*, 1974; Ploog *et al.*, 1963). This behavior is often indicative of dominance relationships; the dominant animal displays to the subordinate one.

Sexual Behaviors

1. Mount/Thrust: the climbing or pouncing of one animal upon the back of another, usually while grasping the waist of the animal being mounted.
2. Position: the orienting of a female by a male into a suitable position for mounting; usually involving the grasping of the female's hips by the male.
3. Present: a female posture involving a crouched orientation of the hind quarters toward a pursuing male.
4. Masturbation: manual or oral manipulations of the erect penis; usually without ejaculation.
5. Genital Inspection: inspecton of an animal's own genitalia.
6. Erection: penile erection.

Scent Behaviors

1. Kickwash: a stereotyped male behavior during which urine is rubbed on the hands and feet and each leg is then kicked across the chest toward the contralateral shoulder, depositing droplets over the animal and substrate (Hopf *et al.*, 1974).

2. Urine Wash: a small amount of urine is deposited on both the subject's hands and then rubbed on the feet. Females as well as males perform this behavior (Hopf _et_ _al._, 1974).
3. Rump Rub: back and forth rubbing of the anogenital region on a substrate. Both males and females perform this behavior (Hopf _et_ _al._, 1974).
4. Back Rub: a rolling, rubbing action of the back on some environmental surface (Latta _et_ _al._, 1967). Both males and females perform this behavior.

(2) Spatial Patterns

In addition to the time-sample behavioral observations of each monkey, a pen mapping technique was utilized to ascertain the spacing pattern of the entire group. A schematic diagram which pictorially represented the double pen living environment, divided into 46 x 46cm squares, was utilized for recording animal locations (see Appendix B). These maps permitted two different analyses: (1) analysis of all subjects' inter-animal distances and (2) analysis of male and female aggregation within the group.

Each square had a number code which was utilized in a computer program for determining inter-animal distances. The pen location code for each animal was transferred to computer cards for processing by the IBM 360-44 computer at Downstate Medical Center, Brooklyn, New York. Each of the study groups was mapped five times a day at predetermined intervals by stationing two observers in front of the pens with spatial diagrams. At a light flash both observers would simultaneously record the location of every animal in the two pens. Therefore each monkey had five numerically-coded locations scored per day. The computer analysis determined the weekly mean distance of each subject from every other subject, thereby permitting the calculation of the weekly means of the male-male, female-female and male-female distances.

The aggregation index was obtained by tabulating the percent of male and female subjects within each of the pens for each map. Thus an average percent per day and per week was calculated.

(3) Vaginal Cytology

In order to assess the effect of estrogen administration on the ovariectomized females of Group 1H vaginal smears were taken once a week for the duration of the hormone induction period and throughout the six week observation period. (See Appendix A for a description of the technique.)

A record of the estrous cycles of the intact females of Group 2 was obtained by vaginal smears taken 3-4 times per week throughout the six week observation period. (See Table XVII.)

Methods of Data Analysis

(1) Social Behavior

Due to the large frequency of zero scores for the opposite-sex social behaviors in all four experimental groups, an analysis of variance could not be used. Opposite-sex as compared to same-sex scores were considered significant if all subjects under consideration showed the same directional pattern. The effect of estrogen treatment on the social behavior of the females and males of Group 1H was evaluated by dependent ± comparison with Group 1.

(2) Spatial Arrangement

A three-way analysis of variance was used to evaluate the same-sex versus opposite-sex distances for the males and females of the four experimental groups. In addition to the evaluation of absolute distances, a differences measure for each subject was obtained by subtracting the same-sex distances from the opposite-sex distances. A two-way analysis of variance was used to evaluate the relative differences between same-sex and opposite-sex distances between males and females of the four experimental groups. Independent and correlated ± tests were used for post-hoc comparisons for both the three-way and two-way analyses of variance.

(3) Vaginal Cytology

The subjects' slides were rated for the type of cells seen (i.e. superficial, intermediate, or parabasal). percent of acidophilic and basophilic cells present, percent of vesicular and pyknotic nuclei, and the presence or absence of leucocytes. The condition of the cells, i.e. whether folded or flat, was also rated. Each female's smears were evaluated independently since cytological patterns are quite idiosyncratic. However, a slide was not considered estrous unless at least 95% of the cells present were cornified superficial cells.

CHAPTER FIVE

RESULTS AND DISCUSSION

The effect of gonadal hormones on spatial relations and social organization will be presented in three sections: (1) Inter-animal distances and aggregation, (2) Social behavior, and (3) Behavior directly related to reproduction. Each section is a qualitative and quantitative comparison of isosexual and heterosexual interaction within and between the four experimental groups. At the end of each section is a discussion of the data presented therein. A final concluding discussion follows the results section.

(1) Spatial Patterns

Inter-animal Distances and Aggregation

All four groups exhibited the social pattern of sexual segregation discussed in the Introduction, in that the distances maintained between same-sex animals were significantly smaller than those between opposite-sex animals ($F=802.7$, d.f.=1/40, $p < .001$) (see Appendix C). However, the magnitude of the difference between same-sex and opposite-sex distances varied significantly among groups indicating that not all groups were segregated to the same extent ($F=6.9$, d.f.=3/40, $p < .01$). In Figure 2 and Table IV the median inter-animal isosexual and heterosexual distances per week are presented. The mean isosexual and heterosexual distances maintained during the six weeks of observation are indicated in Table V.

Group 1

The mean distance between the intact males of Group 1 for the six weeks of observation was 61 cm.. This distance was significantly greater than the distance maintained between the ovariectomized females, which was an average of 23 cm ($p < .01$). The females of this group exhibited a very high frequency of huddling which may have been a major factor in reducing their same-sex distances (see Results, section 2).

The maintenance of separate male and female subgroups was reflected in the heterosexual distances. The mean male-female distance across the six weeks of observation was 102 cm. This distance was significantly larger than that maintained between the males or between the females ($p < .01$). This difference is illustrated in Figure 4 which indicates the mean difference between the subjects' isosexual and heterosexual distances per week. The mean difference for Group 1 was 59 cm.

The mean percent of same-sex animals found in each pen during the six weeks of observations is indicated in Figure 3. The large same-sex aggregation index is indicative of the Group 1 females' tendency to maintain small isosexual distances. During the six weeks of observation, an average of 95% of the females remained in the same pen of the double pen environment. In contrast, the males were considerably more dispersed with an average of 60% of the males in one pen and 40% in the other pen. Although the majority of the males (60%) were located in the same pen with the majority of the females (95%), the males did not occupy the central portion of the pen. They remained primarily beyond the wooden partition which served as a visual block (see Figure 1). Thus, the males were within the same pen but out of the females' social sphere. The segregated pattern in Group 1 was consistently maintained throughout the six week observation period.

Group 1H

The males of Group 1H maintained a mean isosexual distance of 67 cm (see Figure 2, Tables IV and V). This distance was significantly larger than the female-female distance which was an average of 40 cm ($p < .01$). The mean distance of 108 cm between opposite-sex animals was significantly larger than the isosexual distances ($p < .01$). The mean difference between the isosexual and heterosexual distances was 55 cm.

The females of this group tended to be more aggregative than the males (see Figure 3.) An average of 86% of the females were found within the same pen whereas the males were almost equally distributed between the two pens (54%/46%). The utilization of the space within the pens was similar to that described for Group 1. Males generally remained beyond the wooden partition and avoided interactions with the females. The males also showed a preference for a secluded corner on the pen floor. They rarely occupied any of the central areas within the pen. The segregated pattern was maintained throughout the observation.

Group 2

The mean isosexual distance for castrated males in Group 2 was 49 cm and for the intact females was 46 cm. These distances did not differ significantly from one another ($p > .3$); the male-male and female-female distances overlap throughout the six weeks of observation (see Figure 2).

The mean heterosexual distance in Group 2 was 91 cm. This was significantly larger than the isosexual distances ($p < .01$). The mean difference between the hetero- and isosexual distances was 43 cm.

As indicated in Figure 3, an average of 77% of the females were located within the same pen at any given time. The males were more evenly distributed between the two pens, but on the average 53% of the males were in a different pen from the majority of the females. When the males were alone in a pen they utilized the entire area. When females entered the pen the males generally retreated behind the wooden partition. As reported for Groups 1 and 1H, the sexually segregated social pattern was maintained consistently throughout the observation.

Group 3

The isosexual distances maintained by the castrated males and overiectomized females in Group 3 were not significantly different from one another. The mean isosexual distance of the males was 60 cm and that of the females was 58 cm (see Table V). The overlap of male-male and female-female distances throughout the observation can be seen in Figure 2.

The mean opposite-sex distance was 79 cm. This was significantly larger than the isosexual distances ($p < .01$). However, the difference between the same-sex and opposite-sex distances was only 20 cm, smaller than that observed in the other groups. Although the overall distances in this group revealed significant segregation, it should be noted that three males and three females did not consistently conform to this pattern. One female maintained smaller opposite-sex distances than same-sex distances for the six weeks of the study. The other two females had smaller opposite-sex distances during one week of the study. Two males demonstrated a reversal for two weeks and the third male had greater same-sex distances for three weeks of the study.

The average aggregation of the females was 73% and that of the males was 78% (see Figure 3). In general, the male and female majority did not occupy the same pen. However, the males did not restrict themselves to the area beyond the wooden partition even when in the same pen with the females. The males freely utilized the central area whether or not females were present.

Comparison of the Four Groups

The ovariectomized females in Group 1 maintained the smallest isosexual distances of any animals in the study (see Figure 2), significantly smaller than those of Groups 1H, 2 and 3. The Group 1 females had very large huddling scores. This high frequency of huddling tended to reduce the average distances maintained between animals (see Results, section 2). The administration of estrogen to these females (Group 1H) increased their activity levels and, as a consequence, resulted in a significant increase in their isosexual distances from 23 cm to 40 cm ($p < .001$). This approached the mean of 46 cm maintained between the intact females in Group 2 but was still significantly smaller ($p < .05$). The females of Group 3 maintained the largest isosexual distances of any of the females in this study.

Five of the six males of Group 1 also markedly increased their isosexual distances following estrogen treatment of the females (Group 1H), from a mean of 50 cm to a mean of 67 cm. The lowest ranking male did not conform to this pattern. His timidity toward the other males presumably prevented his close association with any of them for the first several weeks of the study. The increase in isosexual distances in both males and females following estrogen treatment was accompanied by an increase in heterosexual distances. The mean of 108 cm for Group 1H was significantly larger than the mean heterosexual distance of Group 1 ($p < .02$). However, the difference between same- and opposite-sex distances did not increase since both increased following hormonal administration.

The castrated males of Group 2 maintained significantly smaller isosexual distances than the intact males of Group 1H ($p < .01$) and the castrated males of Group 3 ($p < .01$). The male-male distances in Group 2 did not differ significantly from the males in Group 1. The Group 3 males maintained significantly smaller isosexual distances than Group 1H males ($p < .05$) and significantly larger distances than the Group 2 males ($p < .01$). No significant difference was found between the same-sex distances of the Group 3 and Group 1 males. Thus, there was no discernible difference between the isosexual distances of castrated and intact males that was independent of the overall social organization of the groups. Therefore, the male-male distances did not directly account for the decreasing magnitude of segregation evident in Groups 2 and 3.

Groups 1H, 1, 2 and 3 represent a continuum on a scale of most segregated to least segregated. This is immediately discernible if one compares the heterosexual distances and difference measures of the four groups (see Figure 2). Such a comparison reveals that Group 1H had significantly

larger heterosexual distances than the other three groups ($p < .05$). Group 1 had slightly smaller heterosexual distances than Group 1H. Group 2 had even smaller heterosexual distances than Group 1 although this difference was not significant. The heterosexual distances of Group 3 were even smaller than those of Group 2 but again not significantly. Thus, a clear pattern emerged; Group 1H and 3 represented significantly different ends of the opposite-sex distance continuum and the other two groups represented intermediate steps.
The difference measures (heterosexual minus isosexual distances) for the four groups revealed essentially the same graded pattern and they also varied significantly ($F=23.7$, d.f.=4/50, $p < .001$). The difference measures for Groups 1 and 1H were significantly larger than the differences measures for Groups 2 and 3 ($p < .05$). The difference measure for Group 2 was also significantly larger than that for Group 3 ($p < .05$). Thus, Group 3 emerges as having the smallest difference between heterosexual and isosexual distances of the four groups.

Discussion: Inter-animal Distances

If one uses inter-animal distances in order to evaluate whether or not a group is sexually segregated, one expects to find that the distances maintained between opposite-sex animals are significantly larger than those maintained between same-sex animals. These data indicate that such a difference existed in all four groups and therefore that sexual segregation is not entirely dependent on gonadal hormones. The degree to which segregation is manifest, however, is significantly influenced by the presence or absence of gonadal hormones.

The degree of segregation manifested by the four experimental groups is most meaningful when first compared with data from the study of intact males and intact females conducted in the same environment (Coe and Rosenblum, 1974). The inter-animal distances of this intact group are presented in Figure 5 and Table VIII. Only the first three weeks of distance data for the experimental groups are presented in order to be comparable to the three weeks of observation by Coe and Rosenblum. All experimental groups maintained smaller inter-animal distances (isosexual and heterosexual) than the intact animals of Coe and Rosenblum. This probably does not reflect an effect of experimental procedures in this study but, rather, a difference in prior familiarity among the animals in the Coe and Rosenblum study. However, the difference between the isosexual and heterosexual distances in Group 1H was virtually identical to that of the intact animals. The mean difference for each group was 55 cm (compare Tables VII and VIII). Thus, the intact males living with hormone-injected females (Group 1H) were comparable to the intact males and females in this respect.

The average difference measure in Group 1 (59 cm, see Table VII) was virtually identical to the above, indicating that ovariectomy had no effect on the difference between hetero- and isosexual distances. The difference measure was significantly smaller ($p < .05$) when the males were gonadectomized (Group 2), and even further reduced ($p < .01$) when both males and females were gonadectomized (Group 3). Thus, gonadectomy appears to have a significant influence on segregation as measured by interanimal distance. Castrating males has a greater influence on desegregation than gonadectomizing females. The maximum degree of segregation which was observed in Groups 1 and 1H, in which the males were intact, reflected the fact that intact males avoided heterosexual interaction regardless of the females' hormonal status. In Group 1 the females were ovariectomized and in Group 1H these same females were receiving estrogen. In Group 2, in which males were castrated and females were intact, segregation, as reflected in the difference scores, was appreciably less. This diminution of segregation in Group 2 reflected the castrated males relatively increased acceptance of female approach.

A further diminution of segregation, again as reflected by the difference measure, is seen in Group 3. This was a direct result of increased male and female interaction and again the castrated male's increased acceptance of female approach. Thus a continuum emerges in regard to the degree of segregation manifested by the four groups. Groups 1 and 1H were maximally segregated (in comparison to intact males and intact females). Group 2 was somewhat less segregated and Group 3 was significantly less segregated.

Segregation in Saimiri appears to be based on separate, but not isolated, male and female social spheres. Thus, segregation in absolute terms, i.e., the opposite-sex distances, is always dependent upon the spatial relations maintained by the male and female subgroups. The degree to which the females stay clustered or dispersed influences the heterosexual distances. If the females are very close to each other, the males can be absolutely closer to them while still maintaining the segregated pattern.

This perspective also applies to the aggregation data. The low activity levels of the Group 1 females (inferred from very large huddle scores) resulted in minimal movement between and around the pens. Had the males not utilized the same pen as the females, their social spheres would have indeed been very isolated from one another. The estrogen-induced increase in activity of the Group 1H females resulted in increased mobility both between and around the pens. The males also responded with an increase in activity between the two pens.

The intact females of Group 2 were very active within and between the two pens, utilizing the central portions of both. Therefore, in order to remain segregated the majority of castrated males rotated between pens to remain in a different pen from the majority of the females. Although the males and females of Group 2 were essentially segregated, the difference scores indicated that the males and females of this group were significantly closer than the males and females of Groups 1 and 1H. Independent, segregated but not isolated male and female social spheres were thus maintained in groups 1, 1H, and 2 but not in Group 3 where both males and females were gonadectomized. The spatial relations of the females, including their activity levels, isosexual distances, and aggregation tendencies appeared to be pivotal to the manner in which segregation was maintained since the males appeared to array themselves around the female social core.

In Group 3 all subjects had significantly smaller difference measures than the other groups. In fact, three of the males and one female did not exhibit inter-animal distances typical of the segregation pattern. These subjects were quite active and utilized the central area of one pen. In this case the male and female "desegregated" coalition became the pivotal group around which the other animals distributed themselves. Thus, the smaller degree of segregation maintained in this group was due to the majority of the females who utilized the pen with fewer males.

(2) Social Behavior

Analyses of the social interactions between animals indicated similarly to the inter-animal distance data that all groups were segregated. The occurrence of huddle, contact and proximity was significantly greater between same-sex animals than between opposite-sex animals. Huddle, contact and proximity represent three degrees of intimacy between animals, with huddle the greatest and proximity the lowest. The occurrence of heterosexual interactions in each of these behaviors was significantly different in all four groups. Male-female proximity scores were significantly higher than male-female contact and male-female huddle scores.

Group 1

The males of Group 1 exhibited a stable dominance hierarchy. The hierarchy was determined by the direction of genital displays within the group. The direction and number of displays between males for the six weeks of observation are indicated in Figure 6. The dominant male (303) was somewhat aloof from the other males and was frequently observed sitting separately from them. Consequently his huddle and contact scores were somewhat lower than those of the other males. The lowest-ranking male (285) remained extremely peripheral to the other males and also had low contact and huddle scores. At no time during the study was an attack upon him observed and he never sustained any wounds. Nevertheless, he spent most of the time alone and rarely let any animal, male or female, within proximity. The male display hierarchy also indicates that the two trios, which were familiar prior to the study, maintained their prior affiliations. All the animals of one trio (303, 285, 329) became dominant over the other trio and, in fact, their displaying was directed primarily towards the previously unfamiliar males.

The within sex social interaction matrix for the group is indicated in Figure 7. Each cell represents the total occurrence of that behavior between subjects. Contact and huddle scores within the two familiar male trios were consistently higher than scores between members of the previously unfamiliar trios. Proximity scores do not reflect this trend, indicating the less 'intimate' nature of this behavior as compared to huddle and contact. It is interesting to note that the most dominant male (303) had no interactions with the least dominant male (285). The frequency of aggression between the males was very low. There were no serious fights involving biting and only three instances of manual aggression occurred during the six weeks of observation. Two of these three instances of manual aggression occurred between previously familiar animals and one occurred between previously unfamiliar subjects.

A dominance hierarchy between the females was not as readily apparent as that between the males. Genital displays between the females rarely occurred. However, observations indicated that two females, one from each previously familiar trio, became codominant over the other females. Female #206 may have been slightly more dominant than #204 as indicated by the only two instances of female-female displays observed. Both females were jointly responsible for the majority of female to male aggression which occurred in response to 'perceived' male incursions upon female personal space.

In contrast to the preference pattern of the males, the females did not maintain a consistent preference for their previously familiar partners. Their huddle and contact scores indicated that new partner preferences developed across the prior familiarity lines (see Figure 7). The females appeared to have become a more cohesive and integrated group than the males.

A comparison of isosexual and heterosexual huddle, contact and proximity scores revealed a significantly higher frequency of same-sex interaction as compared to opposite-sex. The preference for same-sex social partners was indicative of the sexual segregation. The total frequency per subject of same-sex and opposite-sex huddle, contact and proximity is presented in Table XI. The mean same- and opposite-sex affiliative contact score per week is indicated in Figure 8. The mean affiliative contact score between males and females was near zero across the six weeks of observation in contrast to the male-male mean of 23 and the female-female mean of 32.

The mean same- and opposite-sex proximity scores per week are indicated in Figure 9. The male-male mean was 4, the female-female mean was 3 and the male-female mean was 1. Although the same-sex proximity score was consistently higher than the opposite-sex proximity score, the difference between the two was not as dramatic as that of contact and

and huddle (see Table XI). These data indicate that both male and female *Saimiri* are more likely to come into proximity with a monkey of the opposite-sex than to establish contact or huddle. This can be easily seen if one compares each subject's opposite-sex scores for contact, huddle and proximity (c.f., opposite-sex huddling did not occur) (Table XI).

The percent of the observation time in which isosexual and heterosexual huddle, contact and proximity were seen is indicated in Figures 10, 11 and 12. Female-female huddle was extremely high and observed during 80% of the observation. Male-male huddle was observed during 45% of the the observations. Male-female huddling was never observed.

Same-sex contact behavior occurred less often than same-sex huddle: female-female=5%, male-male = 15% and male-female = 0.3% of the observation. Thus, there was more opposite-sex contact than opposite-sex huddle. Female subjects were observed in proximity during 10% of the observation, males during 12% and males and females during 2%. Again we see that heterosexual proximity occurred more frequently than heterosexual huddle or contact.

The absolute frequency of approach, displace and manual aggression during the six weeks of observation is indicated in Table XII. The percent shown next to displace and manual aggression represents the percent the frequency of these behaviors was in relation to the number of approaches.

Again we can see that social interaction (in this case the number of approaches) was greater between same-sex subjects than opposite-sex subjects. Males appeared somewhat less aggressive toward each other than females were; 2% of the male-male approaches resulted in aggression whereas 10% of the female-female approaches resulted in aggression. We can see also that the females initiated more social interactions with the males than vice versa. In fact, females approached males more than three times as often as males approached females. Of the 13 male-female approaches one or 8% resulted in displacement. Of the 44 female-male approaches thirty-six or 81% resulted in displacement.

Group 1H

Many of the behavioral changes in Group 1H may be related to the sexual activity that occurred (see Results, section 3). The administration of estrogen to the females effected not only the sexual behavior but also the overall social pattern.

The dominance hierarchy of the males in Group 1H did not appear to be perfectly linear. The direction and frequency of genital displays in this group is indicated in Figure 13. The astericks indicate a change in rank following estrogen treatment of the females. The display order was not totally uni-directional and there appeared to be some contest among the middle-ranking males. This shift in the dominance hierarchy appeared to be the result of sexual interest in the estrogenized females. The dominant male (303) continued to maintain an aloof status towards other males. He frequently sat and rested alone.

The same-sex social interaction matrix for this group is indicated in Figure 14. The interaction data for the males indicate that in conjunction with changes in the hierarchy, there were changes in partner preferences. The former low-ranking male, #285, joined the other males in huddle and contact behavior. The previously unfamiliar male trios, now integrated in the dominance hierarchy, were also more integrated in their social partner preferences. The males generally seemed more active, and although they were not specifically aggressive, they did appear more agitated than they had been previously.

The female relationships within Group 1H also underwent change. Social partner preferences were somewhat altered as were the dominance relationships among the females. As was the case in Group 1, no clear hierarchy could be discerned. The females engaged in a 'round robin' of manual aggression and displays. Female #204 who had been codominant with #206 in Group 1 appeared to have dropped in social status. Females # 169, 145 and 206 exhibited mounting behaviors towards other females. General activity was increased, and as with the males, the level of agitation also increased.

In spite of these behavioral changes, the group remained sexually separated (see Figures 8 and 9). Same-sex huddling, contact and proximity scores were significantly larger than opposite-sex scores. The weekly mean score of male-male affiliative contact (a combination of both contact and huddle scores) was 24, the female-female score was 23 and the male-female scores was less than 1 (Figure 8). The weekly mean score of male-male proximity was 7, the female-female score was 6 and the male-female score was 1 (Figure 9). The absolute same- and opposite-sex scores for huddle, contact and proximity for all six weeks are indicated in Table XIII. Again, we see that isosexual interaction is significantly larger than heterosexual. The three different degrees of intimacy reflected by huddle, contact and proximity were evident in the consistently higher proximity scores between opposite-sex animals.

The percent of the observation in which same- and opposite-sex interaction occurred was also indicative of the two primary _Saimiri_ social patterns: (1) segregation is manifest in consistently higher isosexual scores, and (2) proximity, which is the least intimate behavior occurs more often between the sexes than does contact or huddle. Male-male huddle occurred during 37% of the observation, female-female huddle during 43% and male-female huddle did not occur. Contact between males was observed during 28% of the study, female-female contact during 10% and male-female during 1.2%. The pattern of proximity scores was similar but with more heterosexual scores: male-male proximity was 15%, female-female was 10% and male-female was 5%.

The absolute frequency of isosexual and heterosexual approaches, displaces and manual aggressions is presented in Table XII. The percent of approaches that resulted in displacements and manual aggressions is also indicated. The increased activity in Group 1H, compared with Group 1, was reflected in the greater number of approach scores. Social interactions (approaches) was still greater between same-sex subjects. Females initiated more interaction with males than males with females and more males were displaced by these interactions than were females. The number of female-male approaches was 112. The female-male displacement score of 91 represented 81% of these approaches. The number of male-female approaches was 22 and the 2 displacements that occurred represented 9% of the approach tally.

Group 2

The male dominance hierarchy based on the direction and frequency of genital displays is indicated in Figure 15. The hierarchy was not completely linear. As indicated by the matrix, only the low-ranking status of #34 was clear. The initial observations before the death of male #57 indicated that he and #34 were favorite social partners. The prior familiarity of the two male trios resulted in males #24, 421 and 416 asserting dominance over the other male subgroup. Male #98 became incorporated into the hierarchy whereas #34 with no social alliances became fairly peripheral to the other males.

The same-sex social interaction matrix is indicated in Figure 16. The continuing alliance between males #24, 421 and 416 was indicated by their contact and huddle scores. The integration of male #98 into the male social network is also apparent. The comparatively low huddle and contact scores of male #34 was indicative of his low-ranking, peripheral status. The males and females of Group 2 exhibited considerable courtship and mating behaviors, which will be discussed in Results, section 3. It should be noted here, however, that only males #24, 421 and 416 were involved in the sexual activities.

The frequency of female-female genital displays was very low and could not be used as an indicator of hierarchical ranking. However, observations of the direction of manual aggression indicated that female #195 was the most dominant female, followed by a codominant pair, #148 and 279. Female #146 was the lowest ranking female and the object of much female dislike. Her social presence was tolerated primarily by one member of her previously familiar trio (#233).

The few incidences of opposite-sex huddling that occurred in this group were between male #34 and female #146. This may have been due to their respective peripheral positions in regard to their own sex. However, this is purely speculative.

The males and females of Group 2 demonstrated significant preferences for same-sex social partners. This was indicated by the weekly means of affiliative contact and proximity scores (see Figures 8 and 9). The male-male affiliative contact score was 30, the female-female score was 17, and the male-female score was 1. The mean score for male-male proximity was 7, the female-female score was 4 and the male-female score was 2. A comparison of the absolute frequency of same- and opposite-sex scores for each subject indicates that there was a greater frequency of opposite-sex proximity scores than opposite-sex contact or huddle scores (see Table XIV). As indicated in Figure 10, male-male huddle occurred during 41% of the observations, female-female huddle occurred during 45% and male-female huddle occurred during .1%. The pattern of contact scores, as indicated in Figure 11, was similar although the scores are smaller: male-male contact was 15%, female-female contact was 10% whereas male-female contact was 2.2%. Figure 12 illustrates that proximity between males occurred during 16% of the observations, between females during 15% and between males and females during 5%.

The absolute frequency of isosexual and heterosexual approaches, displaces and manual aggressions is indicated in Table XII. In addition, the percentage of approaches that resulted in displacement and manual aggression is presented. Isosexual approaches occurred more frequently than heterosexual ones. Females were more initiative toward males than vice versa. There were 71 female to male approaches. The female-male displacement score was 24 or 34% of the approaches. There were 68 male-female approaches and male-female displacement was 12 or 18% of the approaches.

Group 3

The males of Group 3 never integrated into a six-male social network. The hierarchy as determined from the frequency and direction of genital displays is indicated in Figure 17. The asterick next to male #416 indicates that he probably does not deserve the next to last position in the hierarchy. He has been placed there because he never displayed. One trio (males #421, 24 and 416) was extremely dominant over the other trio. As indicated by the same-sex interaction matrix, contact, huddle and proximity rarely occurred across the two trios (see Figure 18). Male #416 was the least dominant male of his trio. Since contact with the other males was limited, he never displayed to them. Thus, in spite of the fact that his allegiance with males #24 and 421 probably placed him higher in the hierarchy, the absence of display scores necessitated that he be allocated to the next to last position.

The females also did not reveal a fully integrated social network. As indicated in Figure 18, interaction between several of the females was low or nonexistent. The social data of Group 3 reflect a very complex picture.

Three of the males (#24, 421 and 416) and one of the females (#279) became an integrated subgroup. Two other males (#173 and 438) also demonstrated some opposite-sex huddling albeit limited. A comparison of isosexual and heterosexual huddling, contact and proximity scores, as indicated in Table XV, reveals that half the males and one of the females did not show significant preferences for same-sex social partners. The distance data discussed in Results, section 1, indicates that all subjects were relatively closer to opposite-sex animals than were the members of Groups 1, 1H and 2. However, five of the females and three of the males appeared to maintain behavioral segregation.

The weekly mean score of male-male affiliative contact was 23, the female-female score was 18 and male-female was 4 (see Figure 8). The weekly mean score for male-male proximity was 6, for female-female proximity was 6 and for male-female was 2 (see Figure 9). The percent of the observation in which male-male huddle was seen was 47%, female-female huddle occurred during 35% and male-female during 10% (see Figure 10). Male-male contact was observed during 23% of the observations, female-female during 13% and male-female during 3.3% (see Figure 11). The percent of the observation in which male-male proximity was seen was 16%, for female-female it was 20%, and for male-female it occurred during 8% (see Figure 12). A comparison of the opposite-sex scores for huddle, contact and proximity indicated that there were more heterosexual proximity scores than either contact or huddle.

The absolute frequency of same-sex and opposite-sex approaches, displaces and manual aggressions as well as the percent of approaches that displace and manual aggression represent are indicated in Table XII. Social initiation between opposite-sex subjects occurred more frequently than between opposite-sex subjects. Females approached males more often than males approached females. The two instances of male-female displacement represented 8% of the 24 male-female approaches observed. The 34 instances of female-male displacement represented 35% of the 98 female-male approaches.

Comparison of the Four Groups

The social behavior in Groups 1, 1H and 2 indicate that these groups were sexually segregated. All subjects in the three groups demonstrated a consistent preference for social partners of the same-sex in that isosexual huddle, contact and proximity scores were larger than heterosexual scores. A comparison of the opposite-sex scores for huddle, contact and proximity also indicated that in all groups a gradation of heterosexual interaction existed. All subjects were more often in proximity with an animal of the opposite-sex than in contact, and were more likely to be in contact than to huddle.

The ovariectomized females in Group 1 had very large huddling scores and therefore were the least active subjects of the study. Huddling was observed during 70% of the observations. The administration of estrogen to these females (Group 1H) increased their activity and significantly reduced the amount of the same-sex huddling to 43% of the observations ($p < .001$). This level of huddling closely approximated the amount of time spent huddling by the intact females in Group 2. However, the females in Group 1H had higher individual huddling scores than the females in Group 2, indicating that they had more than one huddling partner at any given time. The females in Group 2 huddled with fewer partners at a time and therefore had lower individual scores. The contact behavior of the females in Group 1H also approximated the contact behavior of the intact Group 2 females. In both groups female-female contact occurred during 10% of the observations. The mean individual score for Group 1H females was 15 and the mean for Group 2 was 15.7.

The administration of estrogen to the Group 1 females affected the males of the group as well. The increased general activity reduced the male-male huddling from 45% in Group 1 to 37% in Group 1H. In addition, sexual interest in the females increased, generating apparent agitation activity, which was reflected in the increase of male-male approaches from 188 in Group 1 to 337 in Group 1H. Female-female approaches increased from 117 in Group 1 to 193 in Group 1H. Male-female approaches almost doubled, from 13 in Group 1 to 22 in Group 1H. Female-male approaches more than doubled, from 44 to 112.

In Groups 1, 1H and 2 the females approached males more than males approached females. Female-male displacement was also higher than male-female. In Groups 1 and 1H the intact males were displaced 36 and 91 times respectively. These scores represent 81% of the female-male approaches. The castrated males of Group 2 were displaced on 34% of the female-male approaches.

Group 3, where both males and females were gonadectomized, differed from the pattern observed in the other groups. Half the males and one female did not exhibit sexually segregated behavior. The other males and females did conform to the pattern of the other groups, except for their relatively closer opposite-sex distances. All subjects of Group 3 conformed to the general pattern of more female-male approaches and displacement than male-female. In terms of displacement, the castrated males of Group 3 behaved more like the castrated males of Group 2 than like the intact males of Groups 1 and 1H. The female-male displacement score represented 35% of the female-male approaches (Group 2 = 34%, Group 1 and 1H = 81%).

Discussion: Social Behavior

These data indicate that as long as one sex (either male or female) is intact, gonadectomy of the other sex will not obliterate segregation. When all members of a group are castrated, however, the segregated behavior patterns are totally obliterated in some animals, diminished in others and still maintained by some.

Castrated males, whether or not the females they are with are intact, appear to tolerate their presence to a greater degree than do intact males. In contrast, intact males avoid both intact and ovariectomized females more, as reflected by their displacement scores. Intact males were displaced by 81% of female approaches whereas castrated males were displaced 34% (Group 2) and 35% (Group 3) of the approaches. The differential response of castrated and intact males to the approach and proximity of females played a significant role in the maintenance of or absence of segregation. All but one of the castrated males in Group 3 exhibited some degree of opposite-sex huddling. None of the intact males ever exhibited heterosexual huddling.

Female <u>Saimiri</u> are the primary initiators of heterosexual social interactions as indicated by these data as well as those of Coe and Rosenblum (1974). The latter authors found that female-male displacement was significantly greater than male-female. The intact males in that study tended to avoid interaction with females whereas females were more initiative towards males. If male avoidance is crucial to the maintenance of segregation, its diminution by castration is crucial to the loss of the segregated pattern.

The effect of gonadectomy on the females was less clear. Females interacted primarily with other females. Even though they have been depicted here as the primary initiators of heterosexual interactions, which they are, the majority of their social interactions were with other females.

Females exhibit a strong social network around which the males distribute. In order for desegregation to occur, the females would have to begin initiating more interactions across sex lines. The unity of their social network would also have to be weakened. This would then complement the increased tendency of castrated males to accept females. In the case of the ovariectomized female (#279) in Group 3, this was exactly what transpired. She began to exhibit a marked preference for male rather than for female companionship. That this change was an effect of gonadectomy seems obvious. The data on her as an intact female, when she was observed in Group 2, indicate clear same-sex partner preferences. Her behavior contributed significantly to the fact that an integrated female social network never developed in Group 3.

The hypothesized hormonal influence on behavior and social organization is seen most clearly in the area of facilitating certain behavioral dispositions. The hormones act as a stimulus to elicit specific behaviors from the individual and also serve as a cue to others. The removal of these hormones via gonadectomy presumably removes their facilitatory role on social behavior. The postulated hormonal role in the maintenance of social organization functions in conjunction with the primary organizer of primate social structure, i.e., socialization. Primates are socialized into specific roles and behaviors. The hormones facilitate the expression of behaviors which are established via socialization. The facilitatory role of hormones is clearly evident in the differential response of subadults and juveniles to the socializing adult forces (Coe and Rosenblum,1974). Juvenile and subadult male and female *Saimiri* freely interact, playing and huddling together. There is no difference in the isosexual and heterosexual distances they maintain (see Figure 19). When the juveniles and subadults are exposed to adults, only the subadults segregate. It appears that without the action of gonadal hormones the socialization process lacks significant impact.

The males, however, appear to have a greater dependence upon their hormonal state for the maintenance of appropriate behaviors. Regardless of whether females were intact or ovariectomized, castrated males avoided interaction with females less than intact males, even less than intact males living with ovariectomized females. Thus, these results indicate that gonadectomy has a definite impact upon *Saimiri* social organization (i.e., the maintenance of the pattern of sexual segregation) by affecting to a greater or lesser degree the underlying male and female behavior patterns.

(3) Behaviors Related to Reproduction

Groups 1 and 1H

Prior to estrogen treatment, the vaginal smear of the ovariectomized females in Group 1H revealed a cytological profile typical of gonadectomized females. No proliferation of the vaginal epitheleum was evident. The smears were very thin. There were no acidophilic cells, no superficial cells, and only sparse amounts of parabasal cells and leucocytes.

The first injection of 1 mg of depo-estradiol began to affect the vaginal epitheleum and the beginnings of proliferation were detected by the appearance of cornified cells. However, it was not until after the second injection that the estrogen effect was strong enough to produce 100% cornification. The presence of large, flat sheets of superficial cells in the smears was maintained by the estrogen injections throughout the study.

Estrogen injections affected the behavior of the Group 1H females. As discussed previously (Results, section 2), their activity levels were inferred to have increased, resulting in significantly decreased huddle scores ($p < .001$) and increased isosexual distances ($p < .001$). The females also significantly increased their approaches towards males ($p < .001$). They frequently pursued males, often in a manner that included sexual initiations. In the observations of Group 1, prior to the estrogen injections, there was no evidence of sexual activity. After estrogen administration to the females both males and females exhibited greater agitation and social activity than had been previously seen. The females frequently mounted other females, aggressively chasing and grabbing them.

The increased agitation and activity was also evident in the significant increase of male-male approaches and the changes in the male dominance hierarchy. As indicated in Results, section 2, the middle ranking males shifted position (compare Figures 6 and 13). The dominant male increased his frequency of genital displays as did several of the other males. In addition, an increased level of scent-marking and spontaneous penile erections was also observed (see Figure 20 and Table XVI). Before estrogen was administered to the females, only 11 incidences of scent-marking were performed by males. After estrogen treatment of the females, 32 were seen. The incidence of penile erections also increased from 8 before treatment to 54 after treatment. Other measures, such as masturbation and genital inspection did not significantly increase.

Although the increased activity and agitation of Group 1H appeared to be related to sexual arousal, no mating was observed during the first four weeks of the observation. However, in the fifth week the dominant male (#303) initiated mounting behavior with two of the females. He exhibited the full Saimiri courtship pattern, approaching, chasing and exploring the genitalia of the females. He also exhibited the stereotyped male Saimiri sexual initiation behaviors which include darting back and forth in front of the female just prior to the mount. He continued the mating behavior throughout weeks 5 and 6 of the study. Saimiri males are multiple-mount ejaculators. Although male #303 was observed to mount the same female several times in succession (with intromission and thrusting), an ejaculatory mount was never observed. Other males in the group appeared to exhibit the early stages of courtship behavior, darting back and forth in front of the females, chasing and exploring their genitalia but were never observed to mount. The females approached by these males and mounted by male #303 were behaviorally receptive. They permitted the males to approach and explore their genitalia and performed the squat present of *Saimiri* females.

Group 2

Two of the six intact females in Group 2 became acyclic just prior to the beginning of observations. Therefore, the data presented in Table XVII on estrous cycles are based on the other four females. The mean cycle length for the four females was 7.4 days. Female #148 exhibited the shortest cycle length of 6.2 days and female #146 exhibited the longest cycle length of 8.8 days.

As indicated in Table XVII, one female from each of the familiar trios became acyclic. During the first four weeks of the study, the two familiar pairs (#148 & 218) and #146 & 279) cycled synchronously, except for a disruption in the pattern in week three. By the beginning of week five, however, the four females were cycling synchronously.

The females of Group 2 exhibited sexually receptive and sexually initiative behavior. Like the estrogen-treated females in Group 1H, they approached and pursued the males.

All the males in this group had been castrated post-pubertally five years prior to the study. Nevertheless, three of the five males exhibited sexual pursuits and initiation behaviors toward the females. Two of these males exhibited full mounting behavior, including the species-specific pursuit, darting and mounting behaviors. However, the mounts never included intromission. Although these castrated males had erections, they were unable to obtain full erections and therefore were unable to intromit. Their mounting behavior in relation to the females' cycles is presented in Table XVII. All mounts were within two days of an estrous smear indicating an effect of the female's cycle. The two non-cycling females were not mounted nor was the most submissive female in the group (#146). As in Group 1H, sexual activity was manifest with a great deal of agitation in the group. Long bouts of male-female pursuit and approaches were observed.

No sexual behavior occurred in Group 3.

Discussion: Behavior Related to Reproduction

The sexual behavior exhibited by both the males and females in Groups 1H and 2 and the impact of the resultant activity on social organization within the groups is very much in keeping with previous data from wild, semi-natural and intact laboratory groups (Baldwin, 1968, 1970; Latta *et al.*, 1967). These investigators have described the considerable agitation that accompanies mating. Baldwin (1968, 1970) indicated that males displayed to one another and hotly contested ranks. It appears that in semifree-ranging conditions a high ranking male may get so involved in maintaining his position *vis à vis* other males, that he does not mate. The behavioral differences between Groups 1 and 1H were especially indicative of the differences between *Saimiri* social structure in the non-mating and the mating season. The intact males of Group 1 showed virtually no interest in ovariectomized females and were socially inactive and docile. Following the females' estrogen treatment the males responded to the females and to each other with more interest and agitation. This change was reflected in their approach scores and also by the shifts in the dominance ranks of several of the males. The increased levels of scent-marking behaviors and erections also indicated the increased agitation and sexual interest.

The effect of estrogen on the activity levels of the ovariectomized females, increasing their activity in Group 1H, has also been reported in rodents. Rodier (1971) demonstrated that ovariectomy decreases activity in the female rat and that estrogen replacement will increase their activity levels. Inger (1969) demonstrated a positive relationship between estrous and activity in female rats. Activity in a running wheel was greatly increased during estrous and declined in non-estrous periods.

The three castrated males in Group 2 who maintained sexual interest in the females exhibited behavior similar to that reported for rhesus monkey males who have been castrated (Michael and Wilson, 1974). In both species the males retain the interest and ability to mount but the ability to intromit is impaired. This is apparently the result of degeneration of the sensitivity of the penis due to a lack of testosterone.

The length of the estrous cycles of the intact Group 2 females was similar to that reported by other investigators (Rosenblum, 1968; Wolf *et al.*, 1975). However, the synchronization of the estrous periods has not been reported previously. McClintock (1971) reported a similar phenomenon among women living in a college dormitory. Her study demonstrated that roommates and close friends tended to shift their menstrual cycles in the direction of synchrony and tended to menstruate at the same time. This would indicate that they were also ovulating synchronously. If *Saimiri* regularly synchronize their estrous cycles, this would aid in maintaining breeding seasonality. It would also serve to reduce competition between males and increase breeding success.

The data also indicate that *Saimiri* males rarely show sexual interest in ovariectomized females, unless they are receiving estrogen treatments, whereas intact females are often receptive towards castrated males. Similar findings have been reported for other primate species (e.g., rhesus monkey, Michael, 1972). In terms of the evolution of reproductive behavior, the fact that an equivalent cue concerning the male's hormonal status has not evolved is worth further investigation.

TABLES

Table IV: Median isosexual and heterosexual distance (cm) per week (see Figure 2).

Groups						
1. male-male	67	53	27	62	45	50
female-female	32	19	10	25	25	25
male-female	116	94	104	91	98	77
1H. male-male	64	60	61	54	61	84
female-female	26	33	42	41	45	57
male-female	94	100	108	106	124	116
2. male-male	58	64	39	26	48	42
female-female	56	47	59	17	34	43
male-female	92	97	79	87	92	92
3. male-male	67	61	57	55	43	63
female-female	56	57	57	51	60	62
male-female	99	74	71	74	82	82

Table V: Mean distance (cm) across the six weeks of observation.

Groups		Male	SE	Female	SE	Mean difference between isosexual and heterosexual distances	SE
1.	Male	61	4.2	102	2.1	59	2.6
	Female	102	0.5	23	0.4		0.8
1H.	Male	66	0.9	109	0.3	55	1.1
	Female	109	1.0	41	0.5		1.1
2.	Male	48	0.9	91	1.2	43	1.5
	Female	91	1.6	46	0.7		1.3
3.	Male	58	0.8	79	1.6	20	1.7
	Female	79	1.2	58	1.8		2.1

Table VI: Mean male and female aggregation (%) (see Figure 3).

	Female Majority Pen		Female Minority Pen	
Groups	Female	Male	Female	Male
1	95	60	5	40
1H	86	54	14	46
2	77	47	23	53
3	73	22	27	78

Table VII: Mean difference between isosexual and heterosexual distances (cm) per week (see Figure 4).

	Weeks					
Groups	1	2	3	4	5	6
1	65	57	92	45	57	39
1H	50	50	56	59	73	44
2	31	41	28	68	48	43
3	37	8	13	15	27	14

Table VIII: Median isosexual and heterosexual distances of an intact group of male and female adults (see Figure 5).

	Weeks		
Subjects	1	2	3
male-male	100	69	53
female-female	93	75	60
male-female	141	153	167
Mean difference between isosexual and heterosexual distances	33	83	50

Table IX: Mean affiliative contact score per week (see Figure 8).

Groups						
1. male-male	27	24	18	27	26	14
female-female	38	29	35	28	33	30
male-female	0	0	0.3	0.2	0	0
1H. male-male	22	36	25	27	22	13
female-female	34	25	26	19	22	10
male-female	0.2	0	0.4	0.1	0.1	0.6
2. male-male	25	23	47	32	20	32
female-female	16	14	26	11	17	15
male-female	1.4	1.2	0.5	0.8	0.6	1.1
3. male-male	20	23	19	18	31	31
female-female	19	19	17	14	26	14
male-female	6	4	7	3	3	2

Table X: Mean proximity score per week (see Figure 9).

Groups	Weeks 1	2	3	4	5	6
1. male-male	4	4	4	4	4	4
female-female	3	2	5	4	1	2
male-female	1.8	1.5	1.3	0.3	0.1	0
1H. male-male	9	2	8	3	10	11
female-female	6	6	6	5	6	7
male-female	0	0.7	0.4	1.3	2.4	2.8
2. male-male	7	7	6	6	8	6
female-female	5	6	4	3	3	2
male-female	1.9	1.5	0.7	1.9	1.9	1.3
3. male-male	5	2	4	8	7	8
female-female	3	8	7	5	6	9
male-female	1.3	2.5	2.1	1.7	2.2	1.3

Table XI: Total score of isosexual and heterosexual inter-interaction for each subject in Group 1.

SS = same sex, OS = opposite sex

Subjects	Huddle		Contact		Proximity	
Males	SS	OS	SS	OS	SS	OS
303	68	0	26	2	36	14
329	81	0	42	0	21	0
285	5	0	8	0	3	0
268	105	0	34	4	44	7
234	129	0	37	0	24	2
235	125	0	28	0	24	0
Females						
204	137	0	8	0	24	0
206	184	0	12	0	17	0
169	203	0	6	0	9	0
145	136	0	1	0	5	13
205	195	0	11	0	17	1
415	99	0	7	0	15	8

Table XII: Total scores of approach, displace and manual aggression.

Groups	Behaviors	Male-male	% of app.	female-female	% of app.	male-female	% of app.	female-male	% of app.
1	approach	188		117		13		44	
	displace	16	9%	17	15%	1	8%	36	81%
	man agg.	3	2%	12	10%	2	15%	14	32%
1H	approach	337		193		22		112	
	displace	28	8%	37	19%	2	9%	91	81%
	man agg.	10	8%	19	10%	0	-	5	5%
2	approach	214		184		68		71	
	displace	37	17%	56	30%	12	18%	24	34%
	man agg.	10	5%	26	14%	6	9%	6	9%
3	approach	181		174		24		98	
	displace	37	20%	43	25%	2	8%	34	35%
	man agg.	27	15%	27	16%	3	12%	16	16%

Table XIII: Total score for isosexual and heterosexual interaction for each subject in Group 1H.

SS = same sex, OS = opposite sex

Subjects	Huddle		Contact		Proximity	
Males	SS	OS	SS	OS	SS	OS
303	67	0	34	2	33	13
329	66	0	62	1	36	3
285	101	0	28	3	16	5
268	65	0	64	0	34	9
234	75	0	66	2	50	6
235	71	0	54	1	57	3
Females						
204	61	0	19	4	55	15
206	118	0	13	0	26	4
169	125	0	12	2	37	4
145	105	0	8	2	30	18
205	133	0	19	0	24	4
415	62	0	19	0	12	7

Table XIV: Total score for isosexual and heterosexual interaction for each subject in Group 1H.

SS = same sex, OS = opposite sex

Subjects	Huddle		Contact		Proximity	
Males	SS	OS	SS	OS	SS	OS
98	68	0	37	0	37	4
24	123	0	29	2	28	16
34	31	8	22	5	10	6
421	138	0	36	0	33	2
416	89	0	26	18	23	26
Females						
148	83	0	13	2	22	18
146	61	5	17	0	13	0
279	91	0	19	10	27	16
195	94	0	15	4	29	4
218	67	0	17	6	15	9
233	102	0	13	1	29	2

Table XV: Total score for isosexual and heterosexual interaction for each subject in Group 3.

SS = same sex, OS = opposite sex

Subjects	Huddle		Contact		Proximity	
Males	SS	OS	SS	OS	SS	OS
24	64	40	24	25	74	10
421	45	40	54	17	24	24
416	37	34	23	6	28	19
173	117	0	26	0	7	6
93	171	0	54	0	15	1
438	54	3	47	0	64	4
Females						
195	111	0	28	0	41	4
279	6	102	6	28	32	4
145	107	0	16	0	35	1
415	71	0	12	0	18	2
206	25	0	21	0	32	11
348	103	2	40	1	35	6

Table XVI: Total frequency of male erections and scent behaviors in the presence of ovariectomized females (Group 1) and estorgen-treated ovariectomized females (Group 1H).

	Erections		Scent Behaviors	
Subjects	1	1H	1	1H
303	0	23	2	8
329	4	6	1	3
285	0	0	3	3
268	0	9	4	5
234	0	2	0	8
235	4	14	1	5
Total	8	54	11	32

Table XVII: Estrous cycles of the four cycling females in Group 2.

Days	Familiar		Familiar		Mounts
	148	218	146	279	
1					24 218
3					24 148 (twice)
	E	E			
5					
7					
9					
			E	E	416 218 (twice)
11					
	E	E			24 148; 416 148
13					
15				E	
17					
	E				
19					
21					
					24 279 (twice)
23					
			E	E	
25	E	E			
27					
29					24 148 (twice)
	E	E	E	E	
31					416 279
33					
35					
37					
	E	E	E	E	
39					
41					416 148
43					
	E	E	E	E	
45					
mean cycle length	6.3	7.3	8.8	7.3	

FIGURES

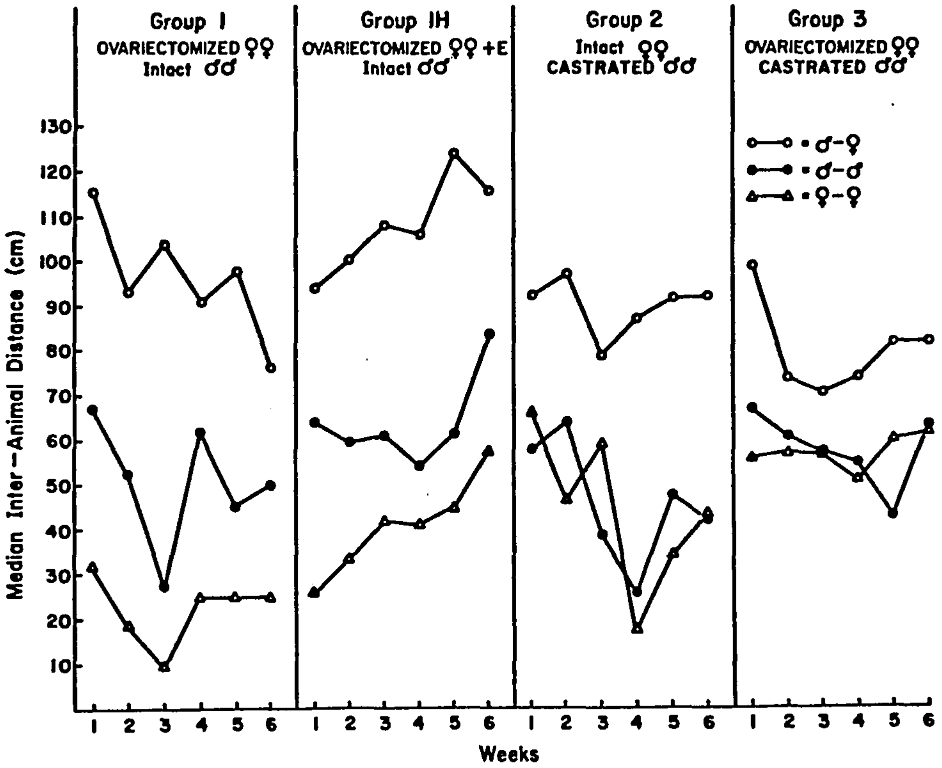


Figure 2: Median isosexual and heterosexual distances for each week of observation. (See Table IV)

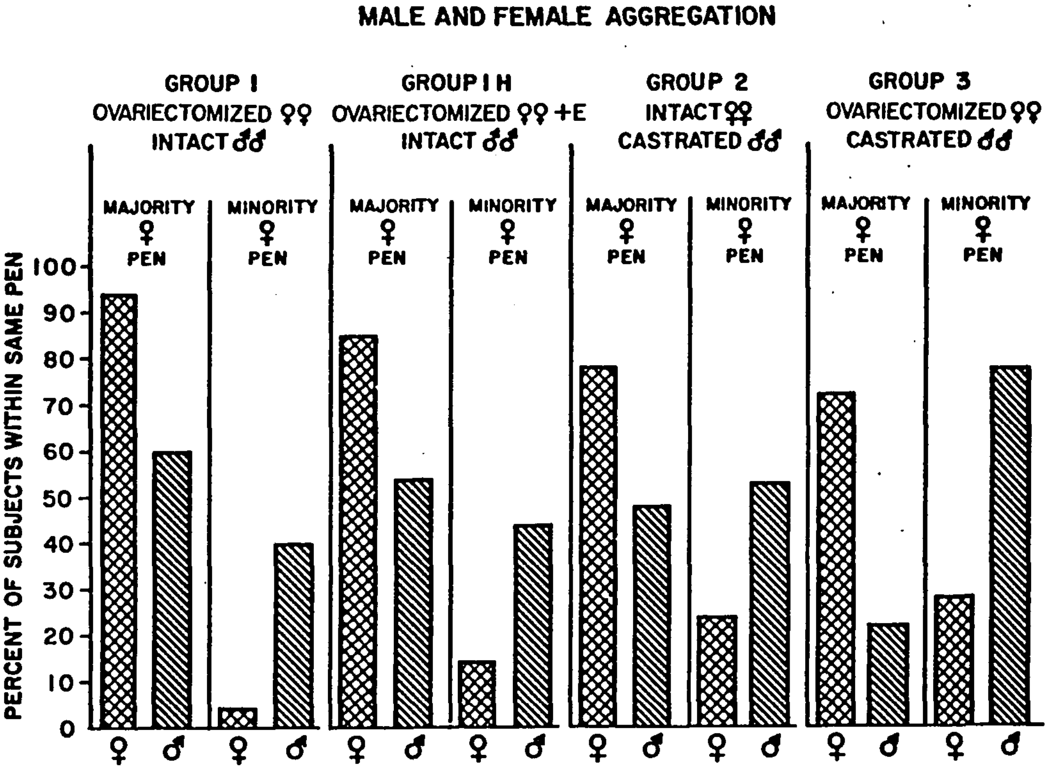


Figure 3: Mean male and female aggregation for each experimental group. The aggregative index indicates the average percent of males and females found in each of the two pens of the living area. (See Table VI)

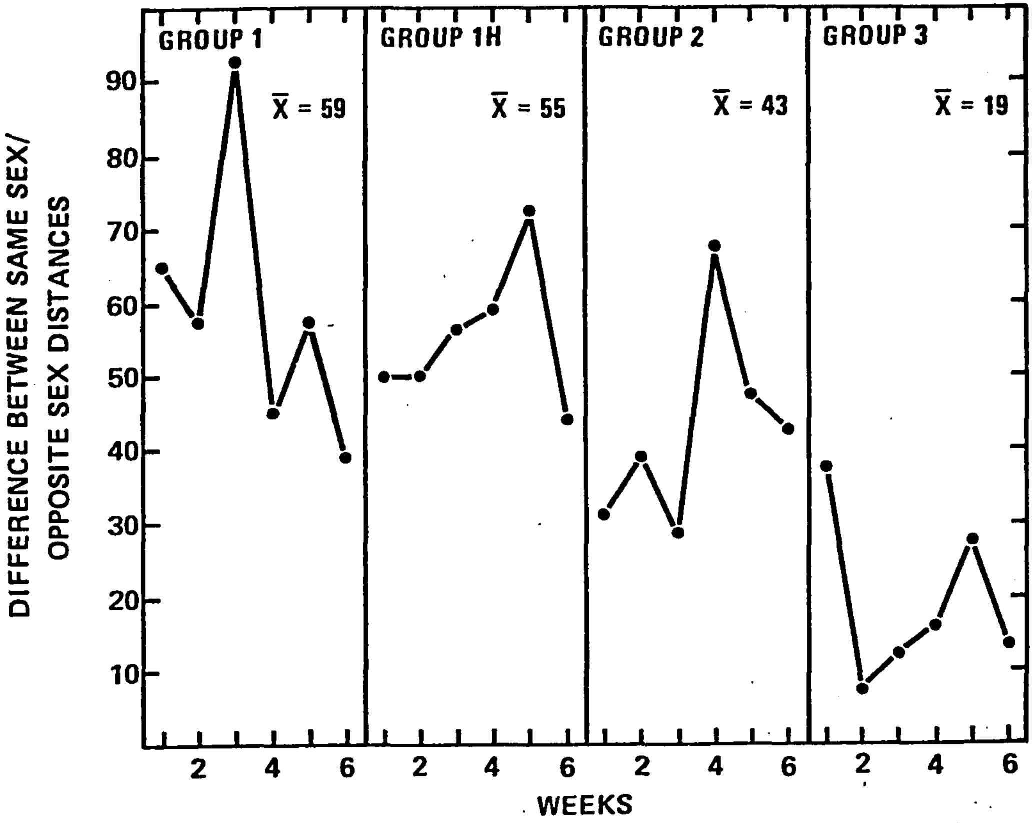


Figure 4: Mean difference between the isosexual and heterosexual distances for each week of observation. (See Table VII)

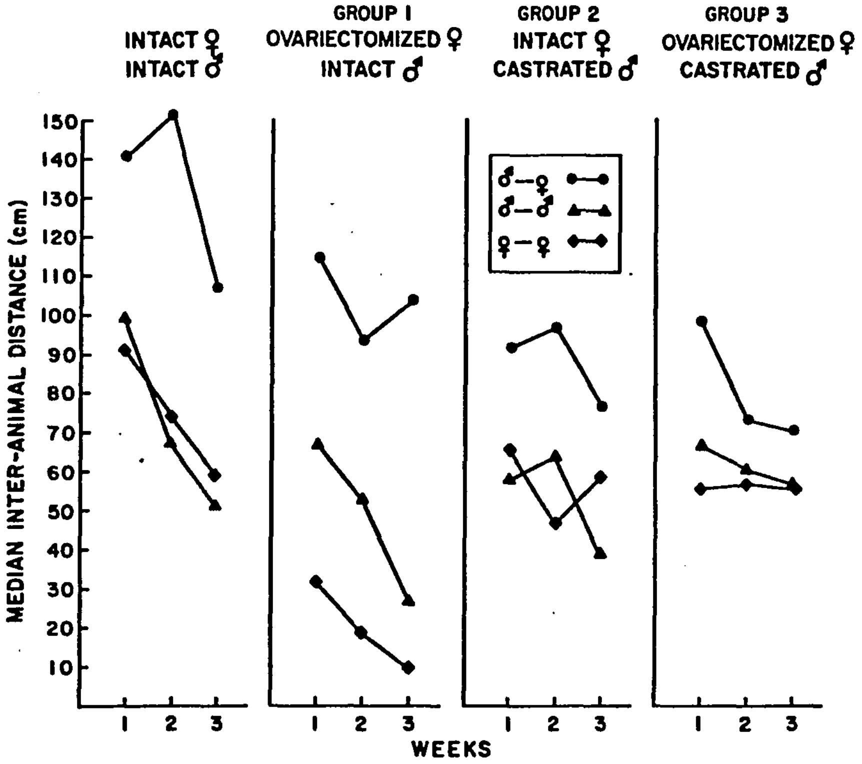


Figure 5: A comparison of the median isosexual and heterosexual distances of a group of five intact males and the five intact females with three of the experimental groups. Note that only the first three weeks of groups 1,2, and 3 have been graphed in order to be comparable to the intact study. (See Tables XVIII and IV)

RECEIVER

INITIATOR

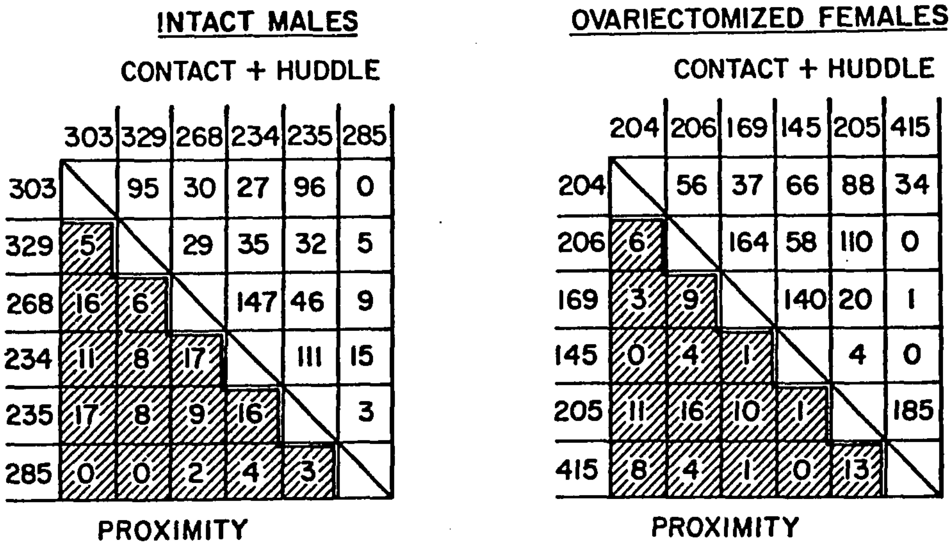
	303	235	329	268	234	285
303		1	0	5	1	0
235			0	3	4	0
329				0	2	0
268					1	0
234						1
285						

GROUP I

MALE DOMINANCE HIERARCHY
BASED ON DISPLAY BEHAVIOR

Figure 6: Dominance hierarchy of the intact males of group 1 based on the frequency and direction of genital display. The number within each cell is the total frequency of genital display for the six weeks of observation.

GROUP I INDIVIDUAL INTERACTION



INTACT MALES

CONTACT + HUDDLE

	303	329	268	234	235	285
303		95	30	27	96	0
329	5		29	35	32	5
268	16	6		147	46	9
234	11	8	17		111	15
235	17	8	9	16		3
285	0	0	2	4	3	

PROXIMITY

OVARIECTOMIZED FEMALES

CONTACT + HUDDLE

	204	206	169	145	205	415
204		56	37	66	88	34
206	6		164	58	110	0
169	3	9		140	20	1
145	0	4	1		4	0
205	11	16	10	1		185
415	8	4	1	0	13	

PROXIMITY

Figure 7: Isosexual interaction matrices for group 1. The number within each cell is the total frequency of contact & huddle (white area) and proximity (shaded area) observed.

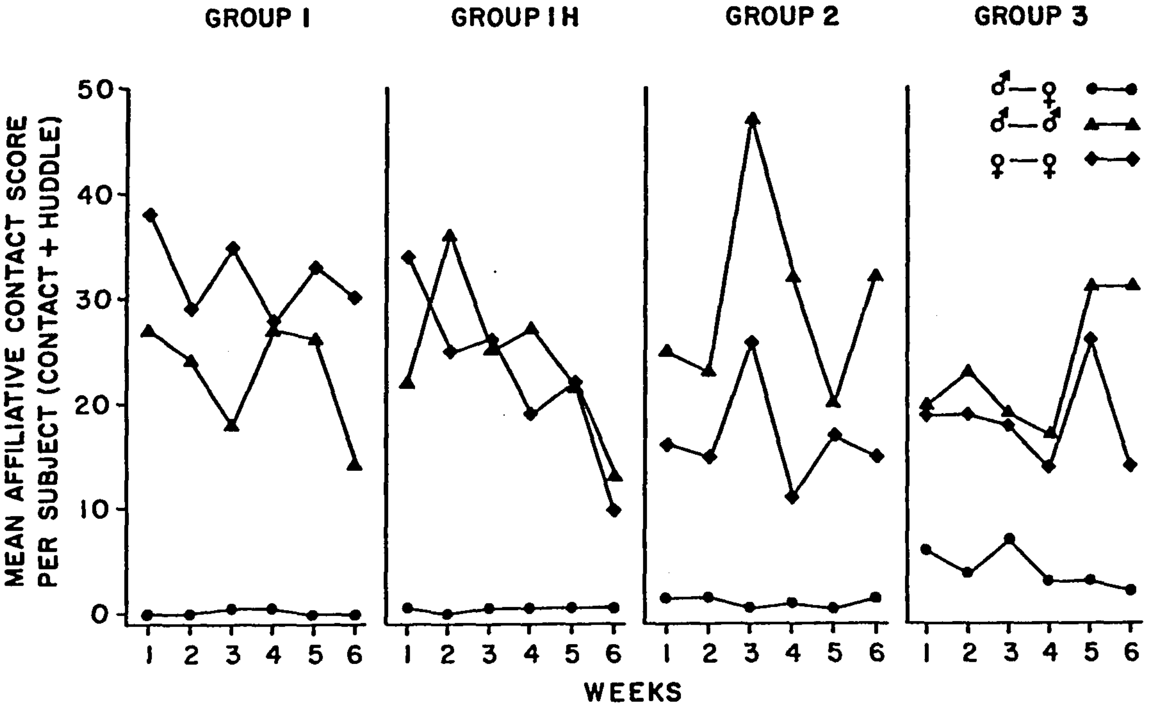


Figure 8: Mean isosexual and heterosexual affiliative contact score for each week of observation. Note that this is on contact and huddle scroes combined.

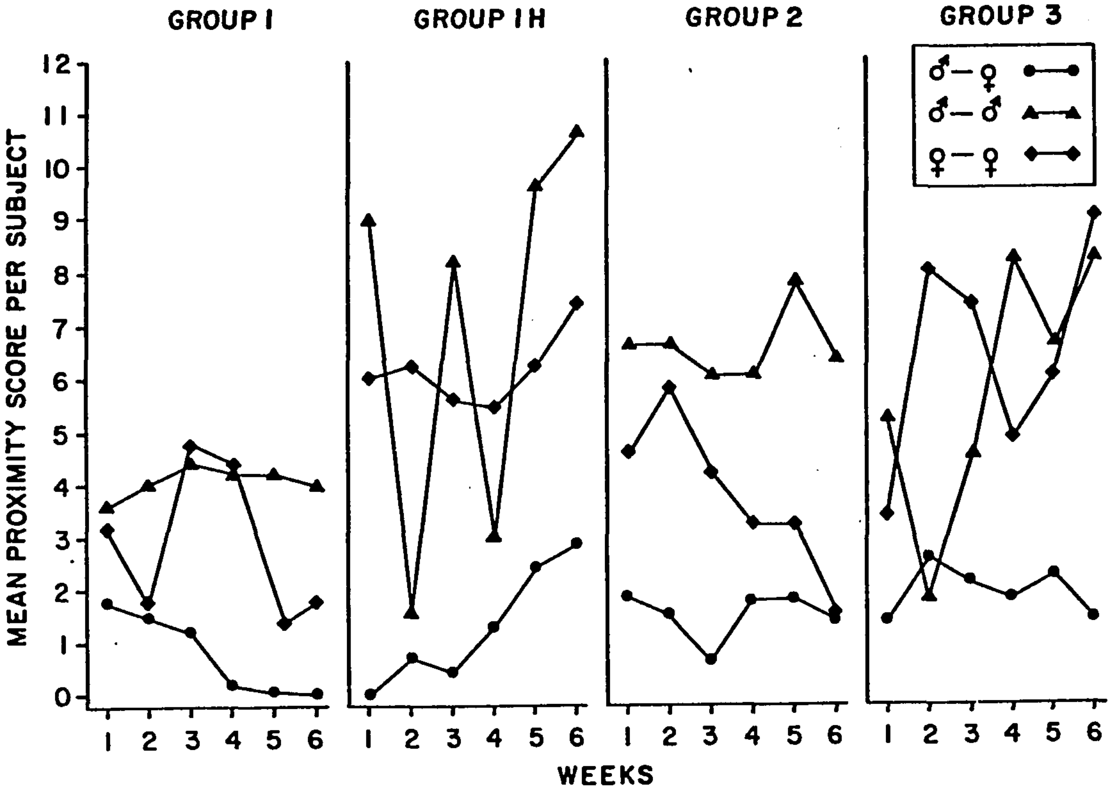


Figure 9: Mean isosexual and heterosexual proximity score for each week of observation. (See table X)

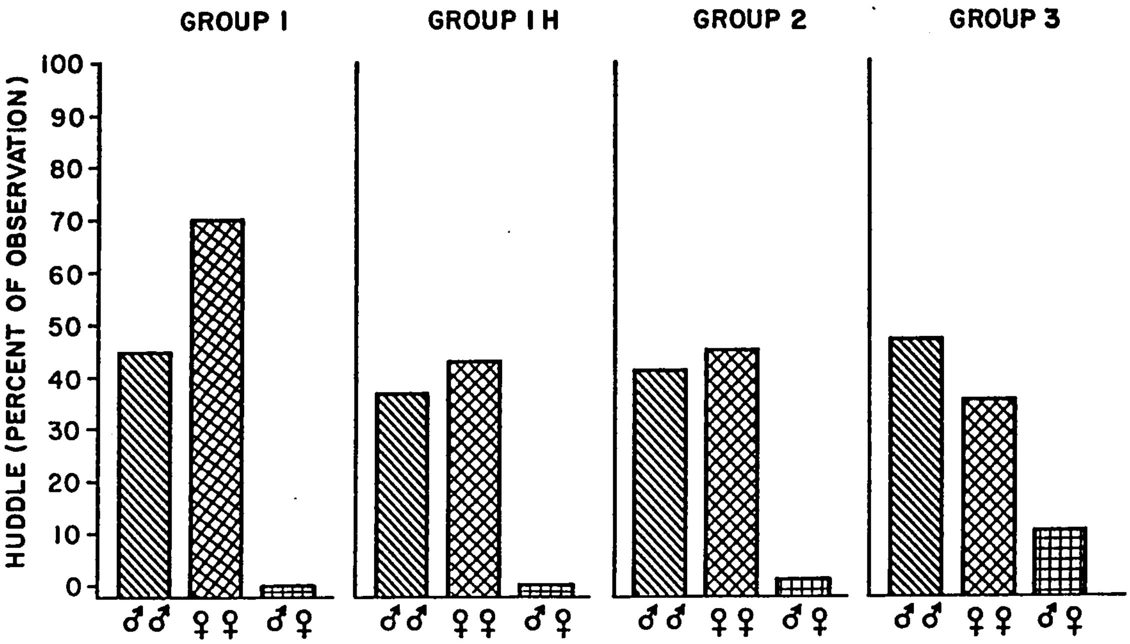


Figure 10: Percent of observation in which isosexual and heterosexual huddling occurred.

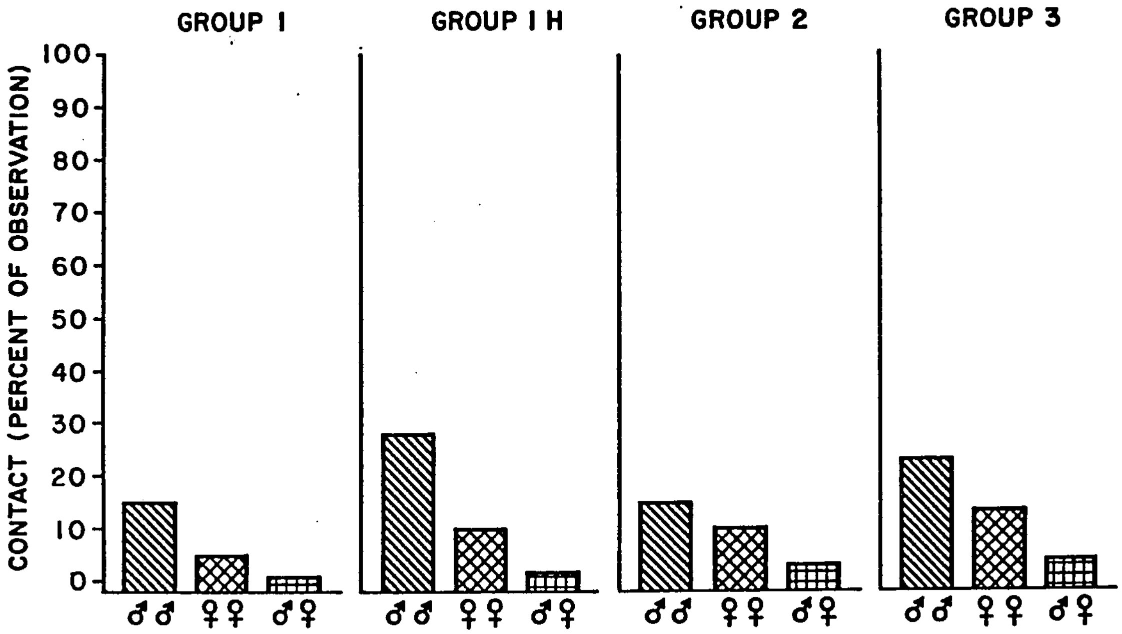


Figure 11: Percent of observation in which isosexual and heterosexual contact occurred.

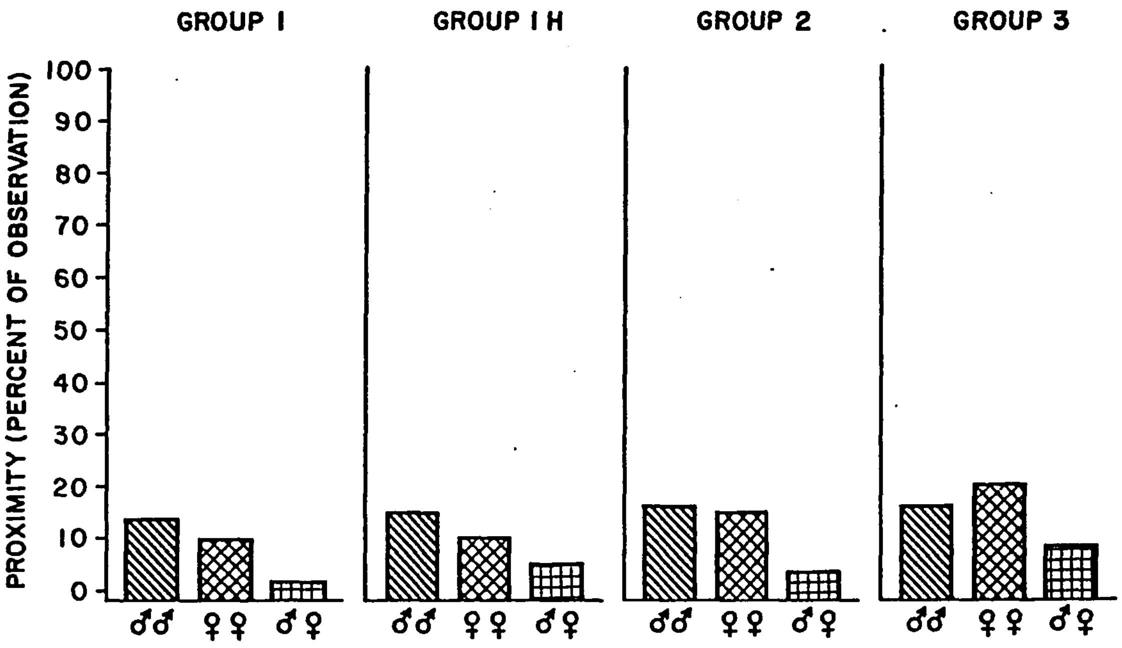


Figure 12: Percent of observation in which isosexual and heterosexual proximity occurred.

RECEIVER

INITIATOR	303	235	234*	268	285*	329*
303		3	2	2	3	0
235			2	2	0	0
234*		1		2	1	6
268		1			0	0
285*				1		1
329*				1		

GROUP 1H

MALE DOMINANCE HIERARCHY
BASED ON DISPLAY BEHAVIOR

Figure 13: Dominance hierarchy of the intact males of group 1H based on the frequency and direction of genital display. The number within each cell is the total frequency of genital display for the six weeks of observation. *indicates a change in rank from group 1.

GROUP 1H INDIVIDUAL INTERACTION

INTACT MALES

CONTACT + HUDDLE

	303	329	268	234	235	285
303		52	34	24	80	29
329	8		42	33	22	78
268	7	17		75	28	70
234	18	15	17		96	70
235	7	20	34	33		20
285	14	5	7	13	10	

PROXIMITY

OVARIECTOMIZED FEMALES + E

CONTACT + HUDDLE

	204	206	169	145	205	415
204		9	9	87	39	9
206	12		131	21	120	5
169	15	16		107	12	5
145	22	1	21		1	11
205	20	17	17	4		128
415	12	4	4	9	11	

PROXIMITY

Figure 14: Isosexual interaction matrices for group 1H. The number within each cell is the total frequency of contact & huddle (white area) and proximity (shaded area) observed.

RECEIVER

INITIATOR

	24	416	98	421	34
24		2	6	0	5
416	2		1	0	7
98	1	1		4	0
421			1		
34					

GROUP 2

MALE DOMINANCE HIERARCHY
BASED ON DISPLAY BEHAVIOR

Figure 15: Dominance hierarchy of the castrated males of group 2 based on the frequency and direction of genital display for the six weeks of observation.

GROUP 2 INDIVIDUAL INTERACTION

CASTRATED MALES

CONTACT + HUDDLE

	98	24	34	421	416
98		52	27	97	19
24	24		30	143	117
34	6	3		4	20
421	23	28	3		87
416	8	10	6	20	

PROXIMITY

INTACT FEMALES

CONTACT + HUDDLE

	148	146	279	195	218	233
148		0	61	91	13	2
146	0		16	0	1	125
279	10	13		31	4	107
195	24	1	16		130	13
218	4	1	1	17		1
233	1	20	21	4	2	

PROXIMITY

Figure 16: Isosexual interaction matrices for group 2. The number within each cell is the total frequency of contact & huddle (white area) and proximity (shaded area) observed.

RECEIVER

INITIATOR

	421	24	173	438	416*	93
421		0	4	6	1	7
24			1	1	1	1
173				0	0	1
438					0	1
416*						0
93						

GROUP 3

MALE DOMINANCE HIERARCHY
BASED ON DISPLAY BEHAVIOR

Figure 17: Dominance hierarchy of the castrated males of group 3 based on frequency and direction of genital display. The number within each cell is the total frequency of genital display for the six weeks of observation. See text for explanation of asterick.

GROUP 3 INDIVIDUAL INTERACTION

CASTRATED MALES

CONTACT + HUDDLE

	24	421	416	173	93	438
24	\	117	86	1	1	1
421	32	\	27	4	10	8
416	20	30	\	0	1	1
173	6	1	1	\	198	52
93	0	3	0	12	\	210
438	1	3	0	32	39	\

PROXIMITY

OVARIECTOMIZED FEMALES

CONTACT + HUDDLE

	195	279	348	415	145	206
195	\	6	128	0	89	20
279	11	\	10	0	0	6
348	14	27	\	112	2	19
415	9	6	11	\	83	10
145	27	3	7	14	\	61
206	21	1	11	10	18	\

PROXIMITY

Figure 18: Isosexual interaction matrices for group 3. The number within each cell is the total frequency of contact & huddle (white area) and proximity (shaded area) observed.

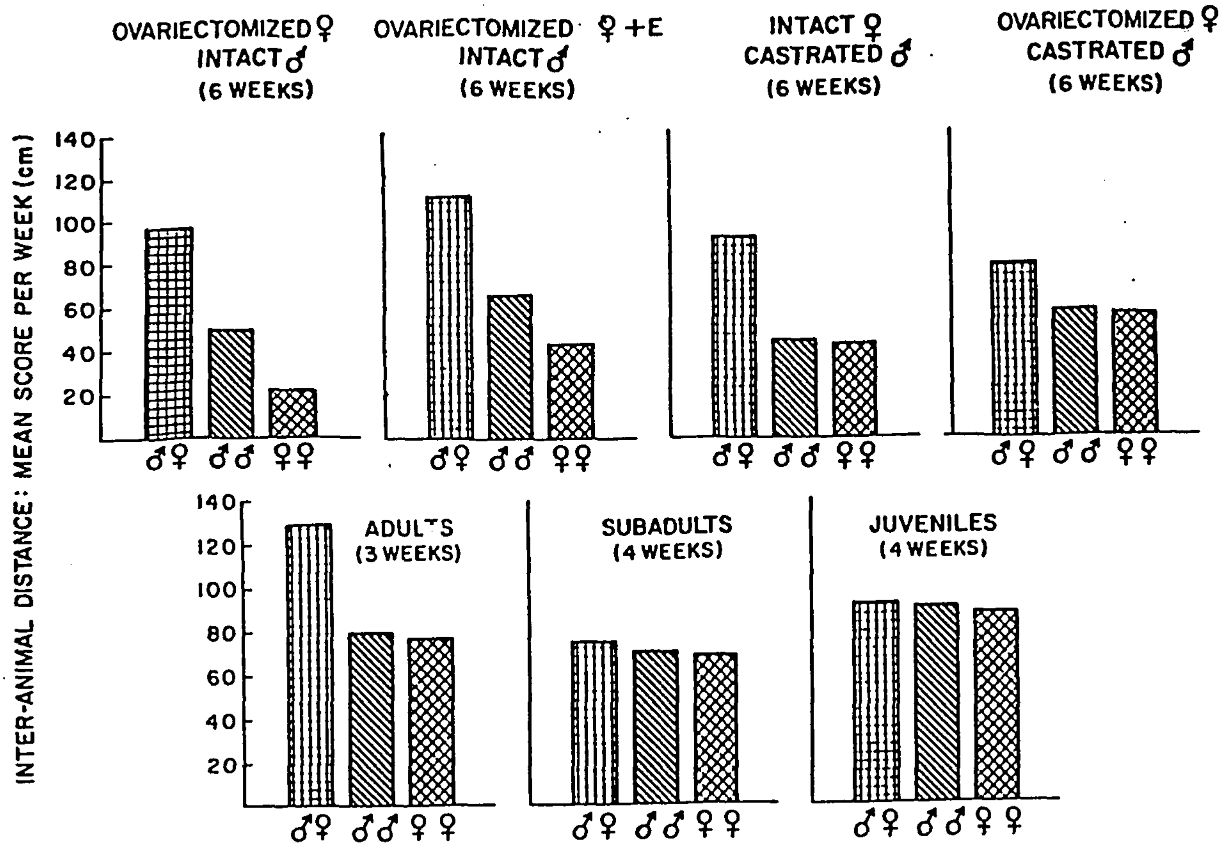


Figure 19: Mean inter-animal distances for the four experimental groups in comparison to intact adults, subadults and juveniles.

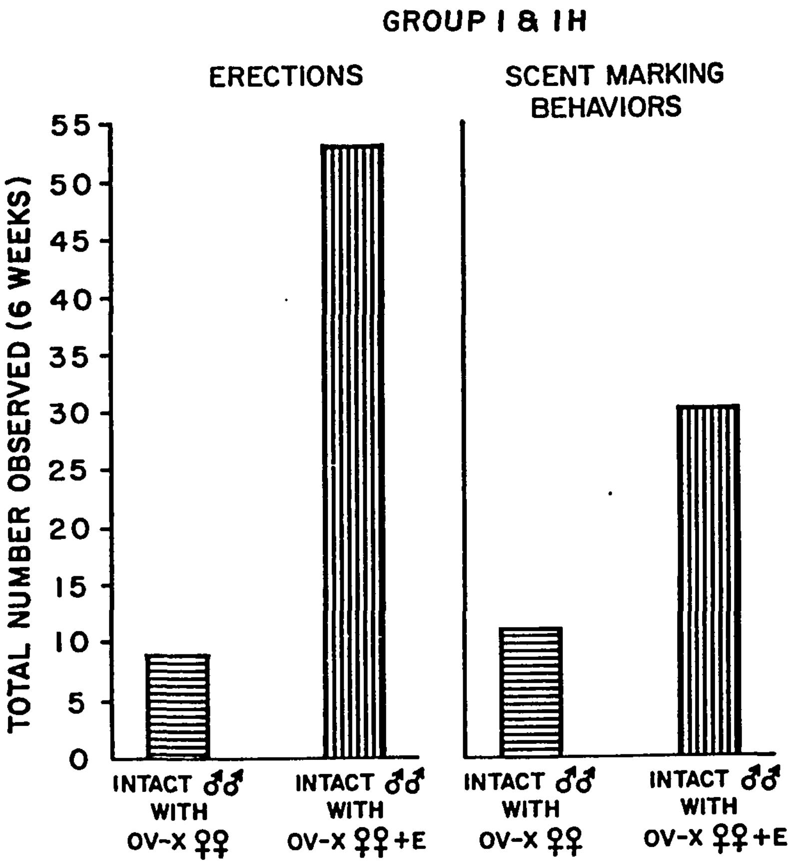


Figure 20: Total frequency of scent marking and erections for the intact males of group 1 and 1H.

CHAPTER SIX

GENERAL DISCUSSION

The data of this experiment indicate that gonadal hormones play a significant role in the maintenance of the sexually-segregated social organization of Saimiri. The absence of gonadal hormones affects the individual behavior patterns of the males and females, altering their interactions, and consequently, altering the relationships between males and females. The data on the inter-animal distances indicated that the general tendency within all groups was towards smaller isosexual than heterosexual distances. Therefore, these data suggest that all groups were sexually segregated. However, a comparison of the heterosexual distances relative to the isosexual distances of the four groups, especially in relation to the distances maintained by an intact group of animals in the same environment, revealed that there was a significant difference in the degree of segregation.

The relative differences between the isosexual and heterosexual distances indicated that a group that contains intact males will be maximally segregated regardless of the hormonal status of the females (compare Groups 1, 1H and Coe and Rosenblum intact study). A group containing castrated males and intact females will be demonstrably less segregated. A group where both the males and females are gonadectomized will maintain the smallest degree of segregation.

The distances maintained between animals are a function of the pattern of social behaviors. In order for heterosexual distances to be reduced, the males and females of a group must be more likely to be in contact with or in proximity with each other than the males and females of a group with relatively greater heterosexual distances. In fact, the amount of heterosexual affiliative contact and proximity were greater in Group 3 where all animals were gonadectomized than in the other groups.

The establishment of contact or proximity between two animals is the result of two behaviors: one animal must approach and the other animal must be willing to accept the approach. The results indicate, indirectly via the interanimal distances and directly via the approach and displacement data, that castrated males are much more willing to accept the approach of a female than are intact males. The difference in the degree to which a castrated male is willing to accept female interaction is crucial to the decrease in the segregation. We may assume, therefore, that avoidance of females by intact males plays a major role in segregation.

The other critical factor in maintaining segregation appears to be the strength of the female social network. The absence of a strong female network in Group 3 contributed significantly to the decrease in the segregation. The defection of one of the ovariectomized females in that group to three of the castrated males had a deleterious effect on the female network and contributed to the establishment of a strong heterosexual network between her and the three castrated males. This heterosexual network became the focus of the group. The smaller heterosexual distances and the increased frequency of heterosexual proximity reflected a generally greater integration of males and females into a unified social network. However, the effect of gonadectomy on females was less consistent than the effect of castration on males. One may speculate that the behavior of male Saimiri is more dependent on hormones than is that of female Saimiri.

It should be noted that the maintenance of segregation, to a greater or lesser degree in all four groups, indicates that other factors in addition to gonadal hormones contribute to the sexually segregated social pattern. Socialization probably plays a crucial role in the development of the appropriate behaviors (Coe and Rosenblum, 1974; Bromley, unpublished data).

The data of this experiment support (at least in Saimiri) several hypotheses introduced earlier in this paper: (1) that hormones have significant effects on behavior, (2) that the influence exerted by hormones on small units of behavior (e.g., male avoidance of females) can and does have significant effects on the social organization as a whole, and (3) that these unit changes alter interactions and consequently relationships (both heterosexual and isosexual). The data also reflect the difference in the male and female social roles in maintaining segregation and the critical balance between attraction and repulsion of conspecifics that underlies any social pattern.

The task at hand is to apply these findings to other primate species and to social organizations. If we review the various social patterns outlined in Chapter 2 with this model in mind we should be able to see how the different levels of social behavior integrate to produce a specific social pattern. We should be able to see how the various behavioral units (i.e. the behavioral repertoire of the species) constitute the building blocks of interactions and how these interactions in turn constitute the building blocks for relationships. It is the patterning of relationships that constitutes the social organization. As indicated by Hinde and Stevenson-Hinde (1976, p. 451):

> The study of social behavior is seen as involving three levels - interactions, relationships, and social structure.

The recognition of the behavioral repertoire as an important variable is seen in the following statement:

> To describe an interaction, it is necessary to specify what the participants are doing together (its content),... (Hinde and Stevenson-Hinde, 1976, p. 451)

Of course the influences exerted by one level on another are not unidirectional. As indicated:

> The distinction between three levels in the conceptual framework of course carries no implications about the direction of causal relationships: interactions influence, and are influenced by, relationships and social structure. (Hinde and Stevenson-Hinde, 1976, pp. 451-452.)

We are dealing with the proverbial chicken or egg question. As indicated previously, innate tendencies are modified and amplified by social forces and may therefore no longer be considered 'innate'. This, like the direction of influence in social organization, is not a biological problem. It is only a problem to us in terms of our inability to explain nature to our own satisfaction. Thus, we may or may not accept the above analysis of social behavior.

If we turn back to the descriptions of social patterns in Chapter 2, we do find that each pattern appears to have a unique configuration of relationships and behavioral repertoires. Pair-bonded species exhibit a continuous male-female relationship exclusively theirs with behaviors also uniquely theirs, e.g., duetting. Unlike most other primates; relationships between females are extremely intolerant and the relationship between parent and offspring may also be unique. The unimale group, as well as the multimale and harem groups can also be seen to be unique configurations of relationships in response to unique interactions and the behavioral units underlying those interactions. As discussed previously, the inability of <u>Erythrocebus</u> males to indicate submission affects their interactions and consequently their relationships with other male conspecifics.

The behaviors of male hamadryas baboons, as they affect females (herding) and other male hamadryas (recognition of the possession of females by subordinate males), seem uniquely suited to such an analysis. As indicated by Nagel (1973) the deficit in the female herding techniques of hybrid male baboons significantly alters interactions, relationships and social organization. A thorough analysis of primate social organization from the standpoint of pinpointing relational differences may be very enlightening.

We generally accept the existence of different social patterns among primates as indicative of adaptations made in response to differing selective pressures. Implicit here is an acceptance and understanding of evolution and natural selection. As discussed in Chapter 2 some behaviors must have some underlying genetic substrate if we accept that behavior does indeed evolve. The relationship between the genes and behavior is a complex one, especially if one is investigating social behavior in primates. It is very difficult to envision the genetic encoding of social organization. However, as indicated previously, only small units of behavior need have a genetic substrate in order for social organization to be affected. The complexity of primate society and the primate's considerable capacity for learning indicate that the behavioral genetic program of monkeys and apes is essentially open. Thus, behavior is somewhat modifiable throughout the life of the individual. As indicated by Manning (1976, pp. 336-337):

> In Waddington's (1957) model of the epigenetic landscape it was the genes which carved out the general pattern and form of the valleys down which the developing organism moves. Behavioral development, particularly in vertebrates, can continue long into an organism's adult life and genes will still set some limits to, and determine some of the directions of its response to the environment.

The picture that emerges is one of loosely encoded behavior, i.e. an open genetic program. Hormones are genetically determined substances that influence behavior. The literature phrases the relationship between hormones and behavior as one of influence which alludes to the characteristics of an open genetic program. In the past, research on the relationship between hormones and behavior has concentrated on the effect of hormones on aggression and on increasing or decreasing copulation frequency or altering copulatory patterns. However, the data of this study suggest that gonadal hormones may influence behavior other than reproductive and aggressive. Attraction between males, between females, and between males and females appears to have been altered. The sexually segregated social pattern appears to be based on specific attractions and repulsions of same-sex and opposite-sex animals and these attractions and repulsions were significantly influenced by gonadal hormones. We are not proposing that all social patterns are dependent upon gonadal hormones, nor that hormones represent the encoding mechanism for all behavior. Rather we are suggesting that gonadal hormones play a significant role in *Saimiri* organization and that they may perform a similar function in other species and that this is worth further research. Does this model apply elsewhere in the primate order or is it a phenomenon peculiar to *Saimiri*?

There are suggestions in the literature that the social behavior and organization of other species may be influenced by gonadal hormones, perhaps not always in the same direction as in the squirrel monkey, but influenced nonetheless. For example, in the siamang family observed by Aldrich-Blake and Chivers (1973) the subadult male was not driven out of his group by his father until the mating season began. There may have been gonadal changes in the adult male which influenced his behavior toward his son. We simply do not know at this point. Nor do we know if gonadal hormones would affect the intolerance female marmosets exhibit toward other female conspecifics. There is evidence that gonadal hormones can affect a wide variety of behavior, such as play behavior (Gordon *et al.*, 1976 ; Rosenblum and Bromley, in press).

Saimiri males and females undergo an annual hormonal cycle that is paralleled by behavioral changes. The levels of circulating steroids in the squirrel monkey are fairly high when compared with levels in other mammals. Thus even the diminished hormone levels during the nonmating season are not unusually low in comparison with circulating hormone levels in other animals. (Therefore gonadectomy should never be equated with the nonmating season.) This in itself may imply a stronger gonadal influence on social organization than is generally found. We may only speculate, however. The behavioral changes evident in *Saimiri* mating and nonmating seasons are seen in other primates. *Macaca mulatta* males undergo an annual testosterone cycle similar to *Saimiri* males and also exhibit behavioral changes that are similar to *Saimiri* (e.g., increased agitation). Although data is not available concerning testosterone cycles in *Lemur catta* and *Galago demidovii*, they too exhibit similar behavioral and mating cycles to *Saimiri* which may imply possible hormonal influences at work in the behavior of these species.

In terms of the initial discussion of the influence of ecology and phylogeny on social organization it is very difficult to deal with *Saimiri*. Its phylogenetic status is not clear. According to Baba *et al.* (1975) and Cronin and Sarich (1975) *Saimiri* diverged from the other platyrrhines very early and may not be closely related to other cebids. Hill (1960) and Rosenberger (personal communication) however, have indicated that *Saimiri* is closely related to *Cebus*. More recently Rosenberger (personal communication) has indicated that *Saimiri* may be related to the Callithricidae more closely than to the Cebidae. It should be noted that the views that *Saimiri* diverged early and is related to *Cebus* and/or Callithricidae are not mutually exclusive. Regardless of its status in relation to the living Ceboidea, *Saimiri* is closely related to the late Miocene *Neosaimiri*. Thus we may speculate that it diverged earlier than the late Miocene, and may have a long independent evolutionary history.

Even if there were no questions concerning its phylogeny, the issue of phylogenetic influence would not be clear since no other New World monkey has the same social pattern. The only other primate with a similar social organization is the Old World monkey, *Miopithecus talapoin*. *Saimiri* and *Miopithecus* are convergent in many respects. In addition to their social organization, these two species are convergent in the niche they occupy, which speaks to the influence of ecology on social organization. Other convergent features shared by the talapoin and the squirrel monkey include relatively small body size, seasonal breeding and fairly large troop size. The *combination* of features shared by *Miopithecus* and *Saimiri* are not found in any other primate. Another important feature possibly shared by these two monkeys is that morphology and/or behavior may be very close to the ancestral condition for their respective groups. Wolfheim and Rowell (1972) have described the talapoin as a cercopithecine 'relict' and *Saimiri* may be close to the ancestral condition for New World primates. All of this as well as that proposed below is admittedly speculative but is being presented as a possibility.

In accepting the solitary social pattern described by Martin (1972) as basal for the primate order we are assuming that the other social patterns evolved from it. Although the social organization of the talapoin and squirrel monkey are significantly different from the basal solitary pattern, they do share some interesting characteristics. The males who are minimally social are organized around a female and infant core. Interaction between adult males and females occurs primarily during mating, which is seasonal. Mating activity is disruptive to social relations between males. It is possible that the social organizations of _Saimiri_ and _Miopithecus_ are very early independent experiments with a nominally multimale pattern. This is not meant to imply that social evolution has been linear and directional but simply that there have been evolutionary experimentations at various stages and this is one of them. We are also not proposing that _Saimiri_ and _Miopithecus_ behavior and social organization have gone unchanged since their respective divergence. Hypotheses such as these merely indicate a point from which perhaps we can extrapolate information concerning ancestral conditions.

It would be interesting to know if the mechanisms that maintain segregation in _Saimiri_ operate in _Miopithecus_. A similar investigation in the talapoin would reveal a great deal about the nature of behavior convergence and the relationships between hormones, behavior and social organization. I am sure that such an investigation would also indicate the way to other research.

Appendix A

Subjects' Laboratory History

Subject's Laboratory Records

FEMALE

#	Arrival in lab	Weights During Study			Medical History
		$\bar{x}$	peak	low	
169	1970 wild born	527	560	500	ox 1970
415	1970 wild born	553	580	530	ox 1970
205	1970 wild born	493	540	450	ox 1970
204	1970 wild born	590	600	570	ox 1970
145	1970 wild born	633	710	580	ox 1970
206	1970 wild born	510	570	480	ox 1970
279	1969 wild born	692	710	680	births: 4/70, 5/71 ovariectomized 10/75
233	1970 wild born	680	750	630	births: 5/72
195	1970 wild born	693	730	670	births: 11/70, 5/72 ox 10/75
148	1969 wild born	683	710	670	births: 5/71, 6/73
146	1969 wild born	597	620	580	births: 3/71
218	1970 wild born	573	590	560	births: 12/70 10/73
348	1970 wild born	597	620	580	no births in lab ovariectiomized 10/75

Appendix A

Subject's Laboratory Records

MALES

#	Arrival in lab	Weights During Study			Medical History
		$\bar{x}$	peak	low	
303	1964 wild born	914	930	900	No remarks
268	1969 wild born	750	800	710	"
329	1970 wild born	918	970	880	"
235	1970 wild born	862	930	800	"
234	1970 wild born	883	970	840	"
285	1971 wild born	653	690	620	"
24	1970 wild born	755	780	730	castrated 1970
416	1970 wild born	669	780	625	castrated 1970
421	1970 wild born	588	620	560	castrated 1970
34	1969 wild born	689	790	650	castrated 1970
98	1969 wild born	600	630	580	castrated 1970
173	1969 wild born	803	830	790	castrated 1970
93	1969 wild born	640	670	620	castrated 1970
438	1969 wild born	663	690	630	castrated 1970

Appendix B

Sample data sheet

Sample pen map

SQUIRREL MONKEY
CASTRATE-INTACT
SEGREGATION STUDY

SUBJ:
DATE:

30 SEC PERIODS

	1	2	3	4	5	6
LOC/ACT						
CONTACT						
PROX						
HUDDLE						
SOSEX G S						

APPROACH						
DISPLACE						
MANUAL AGGRESSION						
DISPLAY						

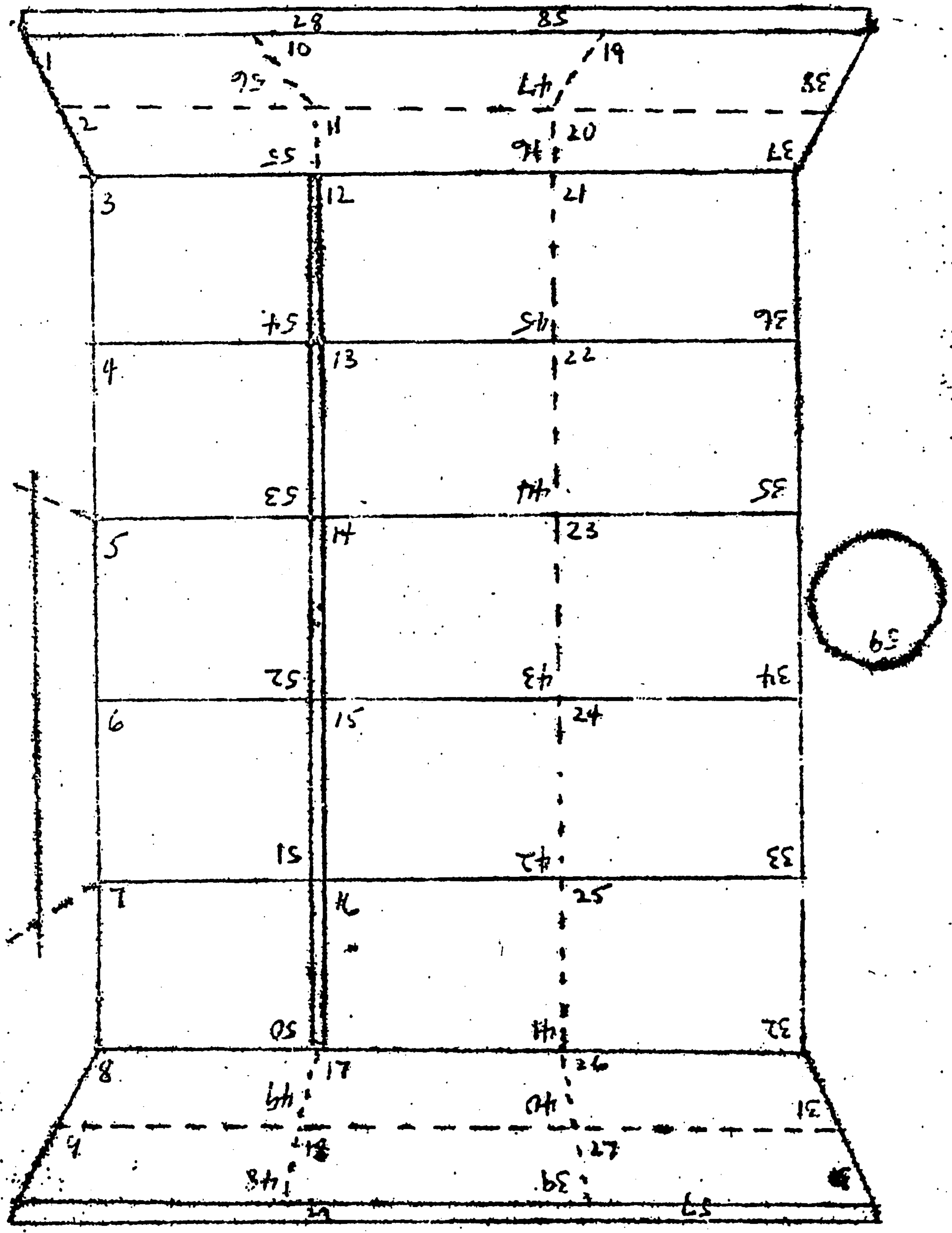
POSITION						
PRESENT						
MOUNT THRUST						

WASH K UR						
RUB B RP						
AUTO H G						
ERECTION						

GROUP/PEN ____

DATE: ____

TIME: ____



60 ____

Appendix C

Computer printouts of analyses of variance

INTER-ANIM DISTANCES

CELL	MEAN	SD	SE
A 1	28.179	13.858	2.890
A 2	31.892	11.531	2.404
A 3	27.092	8.998	1.876
A 4	27.037	5.072	1.058
B 1	30.173	8.955	1.306
B 2	26.927	11.758	1.715
C 1	19.785	6.398	0.933
C 2	37.314	5.397	0.787
AB 1, 1	31.992	10.903	3.287
AB 1, 2	24.367	15.366	4.633
AB 2, 1	34.467	8.368	2.523
AB 2, 2	29.317	13.515	4.075
AB 3, 1	27.092	8.355	2.519
AB 3, 2	27.092	9.597	2.894
AB 4, 1	27.142	4.650	1.402
AB 4, 2	26.933	5.459	1.646
AC 1, 1	16.525	10.042	3.028
AC 1, 2	39.833	3.403	1.026
AC 2, 1	21.075	5.409	1.631
AC 2, 2	42.708	1.637	0.493
AC 3, 1	18.483	1.918	0.578
AC 3, 2	35.700	3.166	0.955
AC 4, 1	23.058	2.291	0.691
AC 4, 2	31.017	3.812	1.149
BC 1, 1	23.196	5.639	1.176
BC 1, 2	37.150	5.587	1.165
BC 2, 1	16.375	5.178	1.080
BC 2, 2	37.479	5.195	1.083
ABC 1, 1, 1	24.017	9.419	4.212
ABC 1, 1, 2	39.967	4.671	2.089
ABC 1, 2, 1	9.033	0.860	0.384
ABC 1, 2, 2	39.700	1.138	0.509
ABC 2, 1, 1	26.233	2.001	0.895
ABC 2, 1, 2	42.700	0.681	0.305
ABC 2, 2, 1	15.917	1.139	0.510
ABC 2, 2, 2	42.717	2.211	0.989
ABC 3, 1, 1	19.083	2.100	0.939
ABC 3, 1, 2	35.100	2.631	1.177
ABC 3, 2, 1	17.883	1.492	0.667
ABC 3, 2, 2	36.300	3.521	1.575
ABC 4, 1, 1	23.450	1.782	0.797
ABC 4, 1, 2	30.833	3.579	1.601
ABC 4, 2, 1	22.667	2.649	1.185
ABC 4, 2, 2	31.200	4.023	1.799

```
INTER-ANIM DISTANCES

SUMMARY OF ANALYSIS OF VARIANCE
-------------------------------
SOURCE        SS          DF           MS           F         P
--------------------------------------------------------------------
     A      377.250        3         125.750       6.601    0.0013
     B      252.813        1         252.813      13.271    0.0011
   AXB      255.438        3          85.146       4.470    0.0086
 ERROR      762.000       40          19.050
     C     7374.500        1        7374.500     802.667    0.0000
   AXC      851.625        3         283.875      30.898    0.0000
   BXC      306.688        1         306.688      33.381    0.0000
 AXBXC      189.000        3          63.000       6.857    0.0011
 ERROR      367.500       40           9.188
--------------------------------------------------------------------

CORE USAGE        OBJECT CODE=   25224 B...
?
```

```
DISTANCE
        D
         '
         FFERENCES

   CELL          MEAN          SD          SE
----------------------------------------------
 A 1            23.325        8.470       2.554
 A 2            21.642        5.686       1.714
 A 3            16.792        3.307       0.997
 A 4             8.367        4.305       1.298
 B 1            13.979        5.511       1.149
 B 2            21.083        8.869       1.849
AB 1, 1         15.983        5.729       2.562
AB 1, 2         30.667        1.691       0.756
AB 2, 1         16.500        2.353       1.052
AB 2, 2         26.783        2.502       1.119
AB 3, 1         16.017        3.415       1.527
AB 3, 2         17.567        3.001       1.342
AB 4, 1          7.417        3.726       1.666
AB 4, 2          9.317        4.624       2.068
----------------------------------------------

DISTANCE DIFFERENCES

SUMMARY OF ANALYSIS OF VARIANCE
-------------------------------
SOURCE        SS        DF          MS          F         P
------------------------------------------------------------------
     A    1620.012       3       540.004     34.812    0.0000
     B     605.637       1       605.637     39.044    0.0000
   AXB     376.422       3       125.474      8.089    0.0004
 ERROR     620.473      40        15.512
       FMAX =   11.480(   8/    5)
------------------------------------------------------------------

CORE USAGE       OBJECT CODE=    24576 BYTES,ARRAY AREA=    56652 B...
?
```

INTACT COMPARISON - DISTANCE DATA

CELL	MEAN	SD	SE
A 1	28.125	13.866	2.891
A 2	31.833	11.567	2.412
A 3	27.125	8.946	1.865
A 4	26.917	4.999	1.042
A 5	40.875	11.526	2.403
B 1	32.317	10.513	1.369
B 2	29.633	12.912	1.681
C 1	21.817	7.177	0.934
C 2	40.133	7.847	1.022
AB 1, 1	32.000	10.985	3.312
AB 1, 2	24.250	15.292	4.611
AB 2, 1	34.333	8.320	2.509
AB 2, 2	29.333	13.634	4.111
AB 3, 1	27.083	8.271	2.494
AB 3, 2	27.167	9.573	2.886
AB 4, 1	27.083	4.573	1.379
AB 4, 2	26.750	5.387	1.624
AB 5, 1	41.083	11.729	3.537
AB 5, 2	40.667	11.316	3.412
AC 1, 1	16.500	10.087	3.041
AC 1, 2	39.750	3.538	1.067
AC 2, 1	21.000	5.447	1.642
AC 2, 2	42.667	1.795	0.541
AC 3, 1	18.583	1.891	0.570
AC 3, 2	35.667	3.249	0.980
AC 4, 1	23.000	2.309	0.696
AC 4, 2	30.833	3.738	1.127
AC 5, 1	30.000	3.082	0.929
AC 5, 2	51.750	4.437	1.338
BC 1, 1	24.533	5.920	1.099
BC 1, 2	40.100	8.051	1.495
BC 2, 1	19.100	7.295	1.355
BC 2, 2	40.167	7.638	1.418
ABC 1, 1, 1	24.000	9.487	4.243
ABC 1, 1, 2	40.000	4.830	2.160
ABC 1, 2, 1	19.000	1.000	0.447
ABC 1, 2, 2	39.500	1.258	0.563
ABC 2, 1, 1	26.167	2.115	0.946
ABC 2, 1, 2	42.500	0.764	0.342
ABC 2, 2, 1	15.833	1.213	0.543
ABC 2, 2, 2	42.833	2.410	1.078
ABC 3, 1, 1	19.167	2.192	0.980
ABC 3, 1, 2	35.000	2.582	1.155
ABC 3, 2, 1	18.000	1.291	0.577
ABC 3, 2, 2	36.333	3.682	1.647
ABC 4, 1, 1	23.500	1.803	0.806
ABC 4, 1, 2	30.667	3.590	1.605
ABC 4, 2, 1	22.500	2.630	1.176
ABC 4, 2, 2	31.000	3.873	1.732
ABC 5, 1, 1	29.833	3.436	1.537
ABC 5, 1, 2	52.333	3.197	1.430
ABC 5, 2, 1	30.167	2.672	1.195
ABC 5, 2, 2	51.167	5.336	2.386

```
INTACT COMPARISON - DISTANCE DATA

SUMMARY OF ANALYSIS OF VARIANCE
-------------------------------
SOURCE          SS          DF            MS           F          P
-----------------------------------------------------------------------
     A      3315.875         4        828.969      43.427     0.0000
     B       216.000         1        216.000      11.316     0.0018
   AXB       296.125         4         74.031       3.878     0.0082
 ERROR       954.438        50         19.089
     C     10065.000         1      10065.000     915.937     0.0000
   AXC       952.625         4        238.156      21.673     0.0000
   BXC       226.875         1        226.875      20.646     0.0001
 AXBXC       274.563         4         68.641       6.246     0.0006
 ERROR       549.438        50         10.989
-----------------------------------------------------------------------

CORE USAGE       OBJECT CODE=...
```

```
INTACT COMPARISON - DIFFERENCES

   CELL           MEAN         SD          SE
----------------------------------------------
 A 1             23.167       8.425       2.540
 A 2             21.417       5.678       1.712
 A 3             16.833       3.362       1.014
 A 4              8.167       4.356       1.313
 A 5             21.833       5.320       1.604
 B 1             15.633       6.457       1.199
 B 2             20.933       8.322       1.545
AB 1, 1          15.833       5.610       2.509
AB 1, 2          30.500       1.708       0.764
AB 2, 1          16.333       2.494       1.116
AB 2, 2          26.500       2.566       1.147
AB 3, 1          16.000       3.317       1.483
AB 3, 2          17.667       3.197       1.430
AB 4, 1           7.167       3.891       1.740
AB 4, 2           9.167       4.561       2.040
AB 5, 1          22.833       4.525       2.023
AB 5, 2          20.833       5.843       2.613
----------------------------------------------

INTACT COMPARISON - DIFFERENCES

SUMMARY OF ANALYSIS OF VARIANCE
--------------------------------
SOURCE         SS         DF           MS            F          P
--------------------------------------------------------------------
      A     1808.598       4         452.149      23.702     0.0000
      B      421.348       1         421.348      22.087     0.0001
    AXB      566.402       4         141.601       7.423     0.0002
  ERROR      953.836      50          19.077
          FMAX =  11.702(  10/    5)
--------------------------------------------------------------------
```

BIBLIOGRAPHY

Aldrich-Blake, F. P. G. 1970. Problems of social structure in forest monkeys, In J. Crook, editor, Social Behavior of Birds and Mammals. Academic Press, London. pp. 79-102.

Aldrich-Blake, F. P. G. and Chivers, D. J. 1973. On the genesis of a group of siamang. American Journal of Physical Anthropology 38; 631-636.

Alvarez, F. 1969. Effects of Sex Hormones on the Social Organization of the Squirrel Monkey. Unpublished doctoral dissertation, Tulane University.

Baba, M. L., Goodman, M., Dene H. and Moore, G. W. 1975. Origins of the ceboidea viewed from an immunilogical perspective. Journal of Human Evolution 89; 89-102.

Baldwin, J. D. 1968. The social behavior of adult male squirrel monkeys (Saimiri sciureus) in a seminatural environment. Folia Primatologica 9; 281-314.

Baldwin, J. D. 1970. Reproductive synchronization in squirrel monkeys (Saimiri). Primates 11; 317-326.

Baldwin, J. D. 1971. The social organization of a semi-free-ranging troop of squirrel monkeys (Saimiri sciureus). Folia Primat. 14; 23-50.

BAldwin, J. D. and Baldwin, J. 1972. The ecology and behavior of squirrel monkeys (Saimiri oergted) in a natural forest in Western Panama. Folia Primatologica 18; 161-184.

Baldwin, J. D. and Baldwin, J. 1976. Primate populations in Chirqui, Panama, In Neotropical Primates Field Studies and Conservation Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates, National Academy of Sciences, Washington, D.C.

Bartke, A. 1975. Effects of inhibitors of pituitary prolactin release on testicular cholesterol stores, seminal vesicles, fertility and lactation in mice. Biol. Reprod. 11; 319-325.

Beach, F. A. Behavioral endocrinology and the study of reproduction. Biology of Reproduction 10; 2-18.

Belt, W. D. and Carazos, L. F. 1971. Fuel structure of the interstitial cells of leydreq in the squirrel monkey during seasonal regression. Anat. Rec. 169; 115-128.

Berustein, I. S. 1969. Stability of the status hierarchy in a pigtail monkey group (Macaca nemestrins). Animal Behavior 17; 452-458.

Von Bertalanffy L. 1950. The theory of open systems in physics and biology. Science 111; 23-29.

Von Bertalanffy L. 1968. General Systems Theory. George Braziler, New York.

Bock, W. J. and von Wahlert, G. 1965. Adaptation and the form-Function complex. Evolution 19; 269-298.

Burton, F. D. 1972. The integration of biology and behavior in the socialization of Macaca Sylvana of Gibralter, In F. E. Poirier, editor, Primate Socialization, Random House, N.Y. pp. 29-62.

Butler, H. 1974. Extraordinary trends in primate sex cycles. Contrib. Primat 3; 2-35.

Candland D. K., Tyrrell, D.S., Wagner, D. S., and Wagner, N.M. 1973. Social preference of the squirrel monkey (Saimiri sciureus). Folia Primat. 19; 437-449.

Carpenter, C. R. 1940. A field study in Siam of the behavior and social relations of the gibbon, In Naturalistic Behavior of Nonhuman Primates by C. R. Carpenter, The Pennsylvania State University Press,University Press, 1964. pp. 145-271.

Carpenter, C. R. 1942. Sexual behavior of free-ranging rhesus monkeys; periodicity of estrus, homosexual, autoerotic and non-conformist behavior. In Naturalistic Behavior of Nonhuman Primates by C. R. Carpenter, The Pennsylvania State University Press, Univeristy Press, 1964. pp. 289-318.

Chalmers, N. R. 1968. The social behavior of free living mangabeys in Uganda. Folia Primatologica 8; 263-281.

Chalmers, N. R. and Rowell, T. E. 1971. Behavior and female reproductive cycles in a captive group of mangabeys. Folia Primat 14; 1-14.

Charles-Dominique, P. 1971. Eco-ethologie des prosimiens du gabon. Biol. Gabonica 7; 121-228.

Charles-Dominique, P. 1972. Ecologie et vie sociale de Galago demidovii, In Behavior and Ecology of Nocturnal Primates, Beih. Tierpsychol. 9; 7-41.

Charlès-Dominique P. 1974. Aggression and territoriality in nocturnal porsimians, In R. L. Holloway, editor, Primate Aggression, Territoriality and Zenophobia, Academic Press, N.Y. pp. 21-48.

Chivers, D. J. 1972. The siamang and the gibbon in the Malay Peninsula, In E. Rumbaugh, editor, The Gibbon and the Siamang, vol 1; Karger, BAsel.

Christian, J. J. 1970. Social subordination, population density, and mammalian evolution. Science 168; 84-90.

Clewe, T. H. 1969. Observations on reproduction of squirrel monkeys in captivity. J. Repord. Fert. Supplement 6; 141-156.

Clutton-Brock, T. H. 1974. Primate social organization and ecology. Nature 250; 539-542.

Coe, D. L. and Rosenblum L., 1974. Sexual segregation and its ontogeny in squirrel monkey social structure. Journal of Human Evol. 3; 551-561

Coe, C. L. and Rosenblum, L. S. in press, Annual reproductive strategy of the squirrel monkey (Saimiri sciureus) Folia Primat.

Conway, C. H. and Sade, D. A. 1965. The seasonal spermatogenic cycle in free ranging rhesus monkeys. Folia Primat. 3; 19-21.

Cronin, J. E. and Sarich, W. 1975. Molecular systematics of the new world monkeys. Journal of Human Evol.

Crook, J. H. L970. Social organization and the environment: Aspects of contemporary social ethology. Animal Behavior 18; 197-209.

Crook, J. H. 1970. The socio-ecology of primates, In J. H. Crook, editor, Social Behavior in Birds and Mammals, Academic Press, London.

Crook, J. H. and Gartlan, J. S. 1966. Evolution of primate societies. Nature 15; 18-19.

Crook, J. H., Ellis, J.E. and Goss-Custard, J. D. 1976. Mammalian social systems: structure and function. Animal Behavior 24: 261-274.

da Cruz Lima, E. 1945. Mammals of Amazonia Vol. 1; General Introduction and Primate, Oficina Grafica Mana LTDA Rio de Janeiro.

Delacour, J. and Mayv, E. 1945. The family anatidae. Wilson Bull. 57; 3-54.

Delsey, E. Evolutionary history of the cercopithecidae. Contrib. Primat 5; 167-217.

Delson, E. and Andrews, P. 1975. Evolution and relationships of the catanhunes, In W. P. Luckett and F. A. Szalay, Phlogeny of the Primates A Multidisiplinary Approach, Plenum Press, N.Y. 1975. pp. 405-446.

DuMond, F. V. 1968. The squirrel monkey in a seminatural environment, In L. A. Rosenblum, and R. W. Cooper, editors, The Squirrel Monkey, Academic Press, N.Y.

DuMond, F. V., Hutchinson, T. C. 1967. Squirrel monkey reproduction; the "fatted" male phenomenon and seasonal spermatogenesis. Science 24; 1067-1070.

Eisenberg, J. J., Muckenhirn, N. A. and Rudran, R. 1972. The relation between ecology and social structure in primates. Science 196; 863-874.

Epple, G. 1970. Maintenance, Breeding, and Development of Marmoset Monkeys (Callithricidae) in Captivity. Folia Primatologica 12; 56-72.

Epple, G. 1972. Social communication by olfactory signals in marmosets, In J. Lucas and N. Duplaiz-Hall, editors, International Zoo Yearbook, Vol 12; 36-42. The Zoological Society of London, London.

Epple, G. 1973. The role of pheromones in the social communication of marmoset monkeys (Callithricidae) Journal Reproduction and Fertility (suppl) 19; 445-452.

Epple, G. 1975. Paternal behavior in saguinus fuscicollis ssp. (Callithricidae) Folia Primatologica 24; 221-238.

Fairbanks, L. 1974. An analysis of subgroup structure and process in a captive squirrel monkey (Saimiri sciureus) Colony. Folia Primat 21; 209-224.

Finger, F. W. 1969. Estrus and general activity in the rat. J. Comp. Physiol. Psychology 68; 461-466.

Fooden, J. 1964. Stomach contents and gastro-intestinal proportions in wild-shot guianan monkeys. American Journal of Physical Anthro. 22; 227-231.

Gartlan, J. S. 1968. Structure and function in primate society. Folia Primatologica 8; 89-120.

Gartian, J. S. 1970. Preliminary notes on the ecology an behavior of the drill Mandrillus leucophaeus, In J. R. Napier and P. H. Napier, editors, Old World Monkeys, Academic Press, London. pp. 445-480.

Gautier-Hion, A. 1971. Repertoire comportemental du talapoin (M. talapoin). Biol. gabon 7; 296-389.

Gautier-Hion, A. 1973. Social and ecological features of talapoin Monkey - Comparison with Sympatric cercopithecines, In R. P. M. Michael and J. H. Crook, editors, Comparative Ecology and Behavior of Primates, Academic Press, London. pp. 147-170.

Gordon, T. R., Rose, R. M., Bernstein, I. S. 1976. Seasonal rhythm in plasma testesterone levels in the rhesus monkey (Macaca mulatter): A three year study. Hormones and Behavior 7; 229-243.

Gould, K. G., Cline, E. M. Williams, W. L. 1973. Observations on the induction of ovulation and fertilization in vitro in the squirrel monkey. Fert. & Steril. 24; 260-268.

Goy, R. W. 1968. Organizing effect of androgen on the behavior of rhesus monkeys, In R. P. M. Michael, editor, Endocrinology and Human Behavior, Oxford Press, London. pp. 12-32.

Goy, R. W. and Phoenix, C. H. 1972. The effects of testosterone propinate administered before birth on the development of behavior in the genetic female rhesus monkeys, In C. Sawyer and R. Gorski, editors, Steroid Hormone and Brain Function, U. of California Press, Berkeley. pp. 193-20.

Hafez, E. S. E. 1971. Reproductive cycles, In E. S. E. Hafex, editor, Comparative Reproduction of Nonhumans Primates, Charles C. Thomas, Springfield. pp. 160-204.

Hall, K. R. L. 1965. Behavior and ecology of the wild patas monkey, Erythrocebus patas in Uganda. J. 2001 148; 15-87.

Hall, K. R. L. 1968. Aggression in monkey and ape societies, In P. Jay, editor, Primates, Holt, Rinehart and Winston, N.Y.

Hill, W. C. O. 1960. Primates Vol IV; Part A, Cebidae Edinburgh University Press, Edinburgh.

Hill, W. C. O. 1966. Primates Vol VI, Interscience, N.Y.

Hude, K. A., and Sterenson-Hinde, J. 1976. Towards understanding relationships: dynamic stability, In K. A. Hundy and P. P. G. Batejan, editors, Growing Points in Ethology, Cambridge U. Press, Cambridge. pp. 45-479.

Hirsch, J. 1967. Behavioral Genetics, McGraw-Hill, New York.

Hutchinson, T. C. 1970. Vaginal cytology and reproduction in the squirrel monkey (Saimiri sciureus). Folia Primat 12; 212-223.

Jay, P. 1965. The Common Langur of North India, In I. Devore, editor, Primate Behavior, Holt, N.Y. pp. 197-249.

Jolly, A. 1966. Lemur Behavior, The Univ. of Chicago Press, Chicago.

Jolly, A. 1972. The Evolution of Primate Behavior, Macmillan, New York.

Jolly, C. and Brett 1973. Genetic markers and baboon biology. J. Med. Primat 2; 85-99.

Jones, C. and Sabatier, P. J. 1968. Comparative ecology of Cercocebus albigena and Cercocebus torguatus in Rio Muni, West Africa. Folia Primat 9; 99-113.

Jones, T. C. and Ma, N. 1975. Cytogenetics of the squirrel monkey (Saimiri sciureus). Federation Proceedings 38; 1946-1950.

Jones, T. C., Throington, R. W., Humm, Adams, E. Cooper, R. W. 1973. Karyotypes of squirrel monkeys from different regions. American Journal of Physical Anthropology, 38.

Jouventin, P. 1975. Observations Sur la Socio-ecologie du Mandrill. Extrait de la Terre et la Vie 29; 493-532.

Kaufman, J. H. 1967. Social relations of adult males in a free-ranging band of rhesus monkeys, In S. A. Altmann, editor, Social Communication Among Primates, The U. of Chicago Press, Chicago. pp. 73-98.

Kinzey, W. G., Rosenberger, A. L., Heisler, P. S., Prowse, D. L., and Trilling, J. S. 1977. A preliminary field investigation of the yellow banded titi monkey, Callicebus torquatus torquatus in Northern Peru. Primates 18; 159-181.

Klein, L. L. and Klein, D. J. 1975. Social and Ecological contrasts between four taxa of neotropical primates, In R. Tuttle, editor, Socioecology and Psychology of Primates, Monton, The Hague.

Koyama, N. 1967. On dominance rank and kinship of a wild Japanese monkey troop in arashiyama. Primates 8; 189-216.

Kummer, H. 1968. "Two Variations in the Social Organization of Baboons," In P. C. Jay, editor, Primates: Studies in Adaptation and Variability, Holt, Rinehart and Winston, N.Y. pp. 293-312.

Kummer, H. 1971a. Primate Societies, Aldine, New York.

Kummer, H. 1971b. Spacing mechanisms in social behavior, In J. F. Eisenberg and W. S. Dillon, editors, Man and Beast: Comparative Social Behavior, Smithsonian Institution Press, Washington, D.C.

Kummer, H. 1974. Distribution of interindividual distances in patas monkeys and gelada baboons, species and sex differences. Folia Primat 21; 153-160.

Kummer, H. Goetz, W. and Angst, W. 1970. Cross-species modifications of social behavior in baboons, In J. R. Napier and P. H. Napier, editors, Old World Moulleys Evolution, Systematics, and Behavior, Academic Press, N.Y. pp. 351-364.

Latta, J., Hopt, S., and Ploog D. 1967. Observations on Mating Behavior and Sexual Play in the Squirrel Monkey (Saimiri sciureus). Primates 8; 229-246.

Luckett, W. P. 1976. Cladistic relationships among primate higher categories: evidence of the fetal membranes and Placenta. Folia Primatologica 25; 245-276.

Manning, A. 1976. The place of genetics in the study of behavior, In P. P. G Bateson and R. A. Hinde, editors, Growing Points in Ethology, Cambridge University Press, Cambridge. pp. 327-344.

Martin, R. D. 1972. Adaptive radiation and behavior of the Malagasy lemurs. Phil. Trans. Roy. Soc. London 264; 295-352.

Mason, W. A. 1974. Comparative studies of social behavior in Callicelous and Saimiri: behavior of male and female pairs. Folia Primatologica 22; 1-8.

Mayr, E. 1958. Behavior and systematics, In Anne Roe and G. G. Simpson, editor, Behavior and Evolution, Yale Univ. Press, New Haven. 341-362.

Mayr, E. L963. Animal Species and Evolution, Bleknap Press, Cambridge.

Mayr, E. 1974. Behavior programs and evolutionary strategies. American Scientist 62; 658-659.

McClintock, M. R. 1971. Menstrual synchrony and suppression. Nature, 220; 244-245.

Mesarovic, M. D. 1968. Systems theory and biology: view of a theoretician, In M. D. Mesarovic, editor, Systems Theory and Biology, Springer - Verlag.

Mitchell, G. and Brand, F. M. 1972. Non paternal behavior in primates, In F. E. Poirier, editor, Primate Socialization, Random House, N.Y. pp. 173-206.

Moyhihan, M. 1962. Hostile and sexual behavior patterns of South American and Pacific laridae. Behaviour Supp. 8; 1-365.

Moynihan, M. 1973. The evolution of behavior and the role of behavior in evolution. Breviora 28; 1-29.

Moynihan, M. 1976. The New World Primates, Princeton University Press, Princeton.

Nadler, R. D., and Rosenblum, L. A. 1972. Hormaonal regulation of the "fatted" phenomenon in squirrel monkeys. Anat. Rec. 173; 181-187.

Nagel, A. 1973. A Comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. Folia Primat 19; 104-165.

Napier, J. R. and Napier, P. 1967. A Handbook of Living Primates, Academic Press, London.

O'Conner R. F. and Wold, R. C. 1971. Seasonal fluctuations in plasma progestins of the squirrel monkey. Amer. Zoologist 11; 649.

Ploog, D. W., Blitz J., Ploog, F. 1963. Studies on social and sexual behavior of the squirrel monkey (Saimiri sciureus). Folia Primat 1; 29-66.

Ransom, T. W. and Rowell, T. E. 1972. Early social development of feral baboons, In F. E. Poirier, editor, Primate Socialization, Random House, N.Y. pp. 105-194.

Reiter, R. J. 1975. Exogenous and endogenous control of the annual reproductive cycle in the male golden hamster: participation of the pineal gland. J. of Exp. Zool. 191; 111-120.

Reguo, J. A. 1970. Androgen secretion by the fetal and neonatal rehsus monkey. Endocrinology 87; 680-687.

Reynolds, V. and Reynolds, F. 1965. Chimpanzees of the Budonga forest, In I. DeVore, editor, Primate Behavior, Holt, Rinehart, and Winston, N.Y. pp. 368-424.

Richard, A. 1974. Intra-specific variation in the social organization and ecology of Propithecus verreauxi. Folia Primat 22; 178-207.

Ripley, S. 1967. Intertroup encounters among ceylon grey langurs (Presbytis entellus), In S. A. Altmann, editor, Social Communication Among Primates, The Univeristy of Chicago Press, Chicago.

Ripley, S. 1970. Leaves and leaf monkeys: the social organization of foraging in gray langurs Presbytis entellus theristes, In J. R. Napier and P. H. Napier, editors, Old World Monkeys: Evolution, Systematics and Behavior, Academic Press, N.Y. pp. 481-509.

Rodier, W. I. 1971. Progesterone-estrogen interactions in the control of activity-wheel running in the female rat. J. Comp. Phys. Psch. 74; 365=373.

Rose, M. D. L973. Quadrupedalism in primates. Primates 14; 337-357.

Rose, R. M., Gordon, T. P., Bernstein, I.S., Catlin, S. F. Androgens and Aggression: a review and recent funding in primates, In Holloway, editor, Primate Aggression, Territoriality and Xenophobia, Academic Press, N.Y. 1974. pp. 275-304.

Rosenblum, L. A. 1961. The development of social behavior in the rhesus monkey. Umpublished doctoral dissertation, U. of Wisconsin, Madison.

Rosenblum L. A. 1968. Some aspects of female reproductive physiology in the squirrel monkey, In L. A. Rosenblum and R. W. Cooper, editors, The Squirrel Monkey, Adacemic Press, N.Y.

Rosenblum, L. A. 1971. Kinship interaction patterns in pigtail and bonnet macaques. Proc. 3rd Congr. Primat. 3; 79-84.

Rosenblum, L. A. 1972. Reproduction of squirrel monkeys in the laboratory. Breeding Primates, Karger, Basel, pp. 130-143.

Rosenblum, L. A. and Bromley, L. J. in press. Hormornal influences on peer interaction in a group of juvenile bonnet macaques (M. radiata).

Rothe, H. 1975. Some aspects of sexuality and reproduction in groups of cative marmosets (Callithrix jacchus).

Rowell, T. E. 1966. Forest living baboons in Uganda. J. of Zoology 147; 344-364.

Rowell, T. E. 1972. The Social Life of Monkeys, Penguin, London.

Rowell, T. E. 1973. Social organization of wild talapoin monkeys. American Journal of Physical Anthropology 38; 593-597.

Rowell, T. E. 1974. The concept of social dominance. Behavior Biology 11; 131-154.

Rowell, T. E. and Dixson, A. F. 1974. Changes in the social organization during the breeding season of wild talapoin monkeys. J. Reprod. Fert. 43; 4190434.

Sabatier, Pi J. 1972. Contribution to the ecology of Mandrillus sphinx of Rio Muni. Folio Primat 17; 404-420.

Sackett, G. P. L973. Innate Mechanisms in Primate Social Behavior, In C. R. Carpenter, eidtor, Behavioral Regulators of Behavior in Primates, Bucknell Univ. Press, Lewisberg.

Sade, D. S. 1965. Some Aspects of parent-off-spring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. American J. of Physical Anthropology 23; 1-17.

Schaller, G. B. 1963. The Mountain Gorilla, U. of Chicago Press, Chicago.

Simonds, S. D. 1965. The bonnet macaque in South India, In I. DeVore, editor, Primate Behavior, Holt, N.Y. pp. 175-196.

Simons, F. L. 1972. Primate Evolution, Macmillan, N.Y.

Southwick, C. H., Beg, M. A. and Siddiqi, M. R. 1965. Rhesus monkeys in North India, In I. Devore, editor, Primate Behavior, Holt, N.Y. pp. 111-159.

Struhsaker, T. T. 1969. Correlates of ecology and social organization among African cercopithecines. Folia Primatologica 11; 80-118.

Struhsaker, T. T. 1975. The Red Colobus Monkey, University of Chicago Press, Chicago.

Sugiyama, Y. 1973. The social structure of wild chimpanzees, In R. P. M. Michael and J. Heds Crook, editors, Comparative Ecology and Behavior of Primates, Academic Press, London. pp. 375-410.

Sussman, R. W. and Tattersall, I. 1976. Cycles of activity, group composition and diet of Lemur mongoz mongoz. Folia Primatologica 26; 270-283.

Thompson, E. B. and Lippman, M. E. 1974. Mechanism of action of glucocorticoids. Metabolism 23; 159-202.

Thorington, R. W., Jr. 1968. Observations of squirrel monkeys in a Colobian forest, In L. A. Rosenblum and R. W. Cooper, editors, The Squirrel Monkey,Academic Press, N.Y. pp. 69-87.

Tilson, R. L. and Tenaza, R. R. 1976. Monogamy and duetting in old world monkeys. Nature 263; 320-321

Tinbergen, N. 1969. Comparative studies of the behavior of gulls (Laridae). Behaviour 15; 1-70.

Turner, C. D. and Banara, J. T. 1976. General Endocrinology, Saunders, Philadelphia.

Word, I. 1972. Female sexual behavior in male rats treated prenatally with an anti-androgen. Physiol. Behav. 8; 53-56.

Wilson, A. P. and Boelkins, R. C. 1970. Evidence for seasonal variation in aggressive behavior by Macaca mulatta. Animal Behav. 18; 719-724.

Wolf, R. H., Harrison, R. M., Martin, T.W. 1975. A review of reproductive patterns in new world monkeys. Lab. Animal Science 25; 814-821.

Wolfheim, J. H. and Rowell, T. E. 1972. Communication among captive talapoin monkeys (*Miopithecul talapoin*) *Folio Primatalogica* 18; 224-255.

Yoshiba, K. 1968. Local and intertroop variability in ecology and social behavior of common Indian langurs, *In* P. Jay, editor, *Primates: Studies in Adaption and Variability*, Holt, Rinehart, and Winston, N.Y. pp. 217-242.