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THE UNIVERSITY OF OKLAHOMA

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SOCIAL ORGANIZATION IN CAPTIVE CHIMPANZEES: THE EFFECTS OF NUMBER OF INDIVIDUALS, SPACE, AND COALITIONS UPON THE DOMINANCE HIERARCHY

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SOCIAL ORGANIZATION IN CAPTIVE CHIMPANZEES: THE EFFECTS OF NUMBERS OF INDIVIDUALS, SPACE, AND COALITIONS UPON THE DOMINANCE HIERARCHY

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SOCIAL ORGANIZATION IN CAPTIVE CHIMPANZEES: THE EFFECTS OF NUMBERS OF INDIVIDUALS, SPACE, AND COALITIONS UPON THE DOMINANCE HIERARCHY

CHAPTER I

INTRODUCTION

> Social Rivalry is inherently density-dependent; the more competitors there are seeking a limited number of rewards, the keener will be the contest, (Wynne-Edwards).

People of a biological persuasion seem to share a common dilemma: they never know what to do with Man. If there is a place for everything in the universe of organisms there seems to be this one exception. The current popularity of the ecological viewpoint leads to the consideration of life forms in their natural environmental context, but when we come to the consideration of Homo sapiens we find the only animal without an ecological niche. The various exponents of either the "man the animal" or the "man the transcendent" approaches usually seem to hold the firm convictions born of self doubt. Articles about man's place in evolution sometimes appear overly persuasive on the basis of relatively little data. Of exceedingly great concern has been man's relationship to the "lower" animals and his place or lack of place in the general scheme of things. As human beings we are conscious of ourselves

and of others, including all life forms. We perceive similarities and differences, draw conclusions, and attempt to solve problems. However, our greatest lack may well be that we are so unable to see ourselves in perspective from a broader point of view than from inside our own skins.

The fact of the relatedness of one animal to others of the same species is shared by all social animals from beetles to man. The forms and functions of intraspecific relatedness are many, varied, and very incompletely understood. It is therefore to be expected that an investigator of the social life of an ant colony will be chary of ascribing the same functions of a division of labor to humans that he does to the ants. On the other hand, as it becomes abundantly clear that there are underlying biological processes extant across species, it would be myopic not to try to apply such information to human life where it seems to fit. Any rigid adherence to either the "something more" or the "nothing but" points of view seems only to get in the way of searching out answers to perplexing problems of social living. An open mind and a flexible but critical attitude toward the findings of behavioral research help keep the whole experimental process alive and relevant.

Among man's closest biological relatives, the nonhuman primates, the one considered closest is the chimpanzee. As has been said of them:

> They are fascinating to watch, far more so in the wild than in captivity. A human observer cannot but feel a certain amount of understanding and sympathy with them because of the many gestures and habits they share with man. (Reynolds and Reynolds, 1965)

Because of their behavioral, biological, and social similarities

to man, chimpanzees provide an invaluable means of studying the animal origins of human beings as well as being highly interesting in and of themselves. Only in very recent years has much been really learned of the social habits of these apes (Goodall, 1963-1965; Kortlandt, 1960; Reynolds and Reynolds, 1965). In captivity most of the work has been carried out with single individuals either isolated from the species or not, but practically no work on chimpanzee groups exists to the present time. More specifically, the social organization of chimpanzees either in the wild or in captivity remains an unknown mystery.

Individual Spacing and Group Behavior

Social organization or disorganization can of course be examined from many different aspects. Some of the major concerns of this investigation will become apparent in this and in succeeding chapters. A main focus throughout will be on the effects of numbers of individuals and the space available upon the social behaviors which comprise social organization in human and nonhuman primates. The research of recent years has led to an increasing interest in the effects of groups upon individuals from street gangs to group psychotherapy, and especially in the rather extreme circumstances of high population density or overcrowding. Such matters as the "population explosion" and related problems have focused concern on the crucial effects of human spacing. There may well be as much danger from the social pollution of overcrowding and overcontact as there is from pollution of natural resources.

Whether the population in question is that of a metropolitan area, a gathering at a mass folk-rock concert, the inmates of a state institution, the animals in a zoo, or chimpanzees in the wild, there are very important questions to be answered about the effects of limited space and increased population on social behavior.

There is more known at the present time about animal "spatial behavior" than there is about human behaviors of similar sorts partly as a result of the necessity for caring for animals under captive conditions. It is well known that if a captive animal is given too little, too much, or the wrong kind of space it is likely to fail to reproduce, become apathetic, fall ill, develop abnormal sexual behavior, become overly aggressive or withdrawn from social contact, turn to self-destructive behavior, or even die. The mechanisms underlying such exigencies are as yet poorly delineated and in fact are usually talked about in the most general terms. What is clearly known is that health and behavior are mightily affected by spatial conditions as they are by other aspects of social living.

In human beings it is also well known, although not so well studied, that social spacing is extremely relevant to the quality of human life possible. Not only does the space available per person become important to consider with regard to interpersonal conflicts and the type of social influences which are effective in mediating such conflicts, but the amount of personal space an individual can claim for himself partly determines his social status as well as represents his status to others. Thus the quality of

interpersonal relationships can hang on something as deceptively simple as the quantity of space within which the individuals live.

Physical Space: The Effects of Crowding

A review of the effects of crowding on human and animal behavior in the literature leads to the conclusion that crowding is not necessarily detrimental for all species in all situations. It seems to depend upon the circumstances and the individuals involved and how well adapted they are to the particular conditions. Even so, a frightening possibility with respect to overcrowding in an animal population came to light with Calhoun's (1962) study of Norway rats. The question was one of the effects of population density on social behavior, and of social behavior on population growth. Enclosed in a quarteracre region with an abundance of food, places to live, and with predation and disease eliminated or minimized, wild Norway rats reproduced at a far lower rate than would be expected without social crowding. The results showed that social stress as a consequence of crowding led to such extreme disruptions in normal maternal behavior that few young survived. A subsequent study of six populations of domesticated albino rats revealed several symptoms of social pathology: females unable to carry pregnancies to full term, females becoming progressively less adept at nest building, males characterized by sexual inappropriateness and cannibalism, and behavior ranging from frenetic overactivity to extreme social withdrawal. It should be noted that greater population density does not automatically mean greater social pathology. The biologist Rene DuBos (1968) refers to Holland's

relatively low crime rate and good physical health in spite of its being one of the most densely populated countries in the world. The ability of both human beings and nonhuman primates to adapt to their surroundings is one of broad flexibility. However, when adults are suddenly placed in living conditions for which they are not prepared biosocially, the results can be tragic.

The significance of social spacing lies not only in the direction of overcrowding of individuals but also in terms of what is optimally suitable for particular situations. Social deprivation or isolation from other members of the species is an extreme in the other direction, or what was called "undercrowding," (Allee, 1951). Understimulation or inappropriate social experience at critical points in development are now thought to be crucial in the suppression of the socialization of humans and subhuman animals. Identification with the appropriate peer group, with the species, and the acquisition of suitable social behaviors depend upon early social experience, (Harlow, 1962; Lorenz, 1952; Scott, 1958). Experiments in which animals are isolated from their species show that later maternal behavior may be drastically altered. Lorenz (1937, 1952) was the first to emphasize the importance of "Imprinting" on later social behavior. He showed that such isolation at critical periods results in an inability of precocial birds to identify with their own group. Similarly Valenstein, Riss, and Young (1955) found that male guinea pigs removed from the species at birth developed deficiencies in sexual behavior. They concluded that sexual behavior in these animals did not become organized into a

behaviorally effective pattern. Harlow (1962) reports that in the monkey (macaque and rhesus) total social isolation during the first year of life produces irreversible social and psychological damage. These monkeys do not play with other monkeys, do not defend themselves when attacked, and do not mate. The development of nonadaptive perceptual ability and defective mothering were found to be consequences of social isolation at birth in sheep, (Lemmon and Patterson, Lemmon, et. al).

In mammals and more particularly in primates including man, a major consequence of crowding seems to be its effect on aggressive behavior. Whether such behavior is described as "aggressive" or in the somewhat more inclusive term "agonistic" the behavior of interest is that related to fighting or attack.

Population density is no doubt of social importance in and of itself. Population spacing becomes most significant, however, in the social context of particular individuals with specific needs in relationship to other particular individuals with their specific needs. The most obvious problem posed to the individual in crowded places is what to do about all those others in case his needs and theirs conflict. The solution arrived at will depend partly on the individual's perception of those in proximity to him as well as the state of his own needs. It will depend in part on the avenues of escape open to him. It will also depend upon the amount of social influence or power he can gather to himself in the situation. An individual's social power includes both the competitive factor with which all social beings must contend

and the amount and quality of influence the individual possesses. Social adaptability depends upon his capacities in this regard.

Social Spacing: Within and Without the Social Group

There are certain terms which describe different spatial variables pertaining to particular species and to the environment surrounding the social group. The terms "territory" and "dominance hierarchy" as well as the terms "status system" and "individual space" are all words used to depict certain features of population dispersion. The study of territorial behavior continues to provide needed information about this important and complex aspect of social organization in avian and mammalian species. A review of the concept "territoriality" by Carpenter (1958) traces the development from observation of the nightingale in 1678 to the work of Howard during the period 1907-1914. Further refinements of the concept are an important part of animal research within the past 30 years (Bourliere, 1956; Burt, 1943, 1949; Crook, 1965; Lack, 1966; Pitelka, 1959; Wynne-Edwards, 1962). Territoriality involves the active defense of an area inhabited by the individual or the group and within which intruders normally flee when challenged. The most aggressive encounters occur on the periphery of the territory bordering that of another individual or group. In a survey of mammalian territories, Burt made an important distinction between "home range" and "territory." The home range is defined as the geographical area over which a group ranges and the territory is the space which is actively defended. Groups may

live in home ranges which overlap, but the boundaries of territories are aggressively defended against intruders. A "core area" is the portion of the home range where activity is most intensely centered: places of feeding, resting, refuge, etc. Tinbergen added the distinction that there are actually two separate tendencies involved: attachment to the geographic site and hostility to the competitors. Following this differentiation permits one to see that both attack and escape may be a part of territorial maintenance. Consequently population dispersion can express mutual avoidance as well as attack (Tinbergen, 1957). Heidiger (1950) brought out the feature that territory is first personalized or rendered distinctive in some way before it is defended.

The term "dominance" does not have so specific an origin or development in meaning and is used to refer to a variety of social encounters in which dominant-subordinate reciprocal exchanges can be observed. The dominant animals enjoy the right of preference over their subordinates in access to food, mates, and space. The nature and expression of dominance interactions are very complex and vary according to the situation. There are diverse subtle and intricate ramifications of dominance behaviors for social dynamics in birds and mammals. Some animal groups become organized into straight-line dominance hierarchies, for instance, while others form patterns of a different form. A straight-line hierarchy is one in which each individual is significantly dominant over all those below him and is subordinate to all those above. Other types of hierarchies which exist in social groups include the triangular, the circular, the central, and the

loosely stratified hierarchies.

The early experimental work of reference on dominance hierarchies is that of the Norwegian scientist Schjelderup-Ebbe (1922) who studied the social behavior of chickens. He described the relationships of all the members of a flock of hens in terms of a social organization referred to as a "peck order." In this type of organization agonistic behavior follows the dominant-subordinate lines of precedence. Each chicken "knows" which other members of the flock he may peck and which others may peck him. Normally a hen attacks only those beneath her in dominance status, and if she is attacked by her social superior she does not retaliate. A dominance order of this sort is thought to provide a social mechanism for the reduction of destructive fighting within the group. This organization is therefore a form of social adaptation which may have evolved for the preservation of group coordination and group effectiveness in living.

Hierarchies have been found to exist in all the classes of vertebrates and in many arthropods as well. Something very much akin to the chicken "peck order" and to the dominance hierarchies of mammals is the "status system" which exists in varying forms within human societies. Whyte (1943) observed:

> Each member of the corner gang has his own position in the gang structure....The leadership is changed not through an uprising of the bottom men, but by a shift in the relations between men at the top of the structure.

Among human institutions and other complex social organizations such as hospitals, prisons, corporations, military establishments,

schools, etc. status or power orders exist in which some individuals enjoy more prestige and authority than others. An analogous situation can be found in the social stratification of urban societies (upper", "middle", and "lower" classes) in which status symbols are manifest through location of neighborhoods, make of automobile, type of occupation, quality of clothing, etc. Many privileges accrue to one's social position in the way of memberships, invitations, spatial priorities, titles, and preferential treatment. A fairly comprehensive description of the national "pecking order" was published by Packard (1959) and many striking and apt analogies can be drawn between human and nonhuman status-seeking behavior.

Within the contained and confined worlds of the mental hospital, prison, and military organization, dominance or status systems may operate as a necessary control of potential aggression arising under stress conditions in which there is a maximum of human contact. Frequent contact between inmates and staff could result in many aggressive encounters which are reduced, perhaps unfortunately sometimes, through rigid status hierarchies. Mental hospitals and prisons are so totally organized around the control of all aspects of human interaction and even solitary behavior that the term "total institution" is particularly appropos (Goffman, 1961). By "total institution" is meant all those closed worlds in which people live in virtual isolation from the "outside" world: reformitories, training camps, concentration camps, monasteries, shipboard, old folk's homes, sanitoriums, etc. The totality of the

influence of such tightly structured social environments upon individuals is so great as to determine their behavior in large part, perhaps even that symptomatic behavior for which they are confined (Goffman, 1961; Szasz, 1961).

Additional concepts are available which serve well as analogies to the concepts of "territory" as well as "dominance." Sommer (1969) discussed the functions of invisible boundaries which appear to play a dynamic role when it comes to how close one individual gets to another. Such boundaries can be demonstrated to exist around each individual in proximity to other people, and to vary with the individual's previous social learning. Such areas of personal space around the individual's body are maintained against intruders:

> The best way to learn the location of invisible boundaries is to keep walking until somebody complains. . . .Like the porcupine in Schopenhauer's fable, people like to be close enough to obtain warmth and comradeship but far enough away to avoid pricking one another.

The personal space which persons in different cultures feel comfortable with or require constitutes a major feature of social distance relations. Sommer (1969) points out that hospital patients have been observed to complain that not only is their personal space and even their very personal bodies violated by nurses, interns, and physicians, but that their "territory" is violated by visitors who ignore the "No Visitors" signs.

A close relationship seems to exist between human territories (ownership) and status positions (social prestige) possibly

because these two aspects of social living often amount to the same thing. One's social standing is judged by his property holdings with regard to quality and to amount, and at the same time his social standing is seen as a "place" in the system which he occupies: a kind of social region. Social and spatial orders function as very similar phenomena:

> In the barnyard the top chickens have the greatest freedom of space and can walk anywhere, whereas lower birds are restricted to small areas and can be pecked by other birds wherever they go (McBride, 1964).

> In human society the social elite possess more space in the form of larger homesites, more rooms per house, and vacation homes. In addition, they have greater spatial mobility and more opportunities to escape when they become tense, uncomfortable, or bored (Sommer, 1969).

Perhaps most importantly, human and nonhuman dominance positions are expressed through appropriate behaviors taking place between interacting individuals. These mutual exchanges between unequal persons reinforce their inequalities and their mutual tacit acceptance of these differences, at least temporarily. It seems logical to consider matters of "individual space" or "social space" as encompassing all the behavior, rights, and extent of social influence possessed by the individual in his group. This space determines the limits of his social freedom within that group. Individual space is not rigid for any individual within a particular group, for the most part, but simply connotes an important feature existing as a part of the social pattern between individuals. The nature of the relationship between them is also of primary

significance, of course, and all relationships undergo changes from time to time. Individual space, interpersonal types of relationship, and communication are dynamically interwoven into the fabric of social life.

Comparison of Free and Confined Populations: Research

Since the 19th century experimental study of the effects of crowding on growth in the water snail, it has been known that overcrowding can have harmful biological consequences (Allee, 1958). There has been a long-held view among the older writings in natural history that group organization must be sufficient to cope with danger and attack under conditions of crowding:

> Living beings not only struggle and compete with one another for food, mates, and safety, but they also work together to ensure to one another these same indispensable conditions for development and survival (Wheeler, 1913).

At the other end of the continuum lie the effects of social deprivation on later behavior, effects that may mean the individual will become unable to mate or reproduce or behave appropriately in social situations. In between these two extremes in social environment there remains to be investigated an area of comparison between species which contrasts the effects of an open versus a restricted environment upon the same or similar populations. Differences between social behavior and organization which arise under conditions of free living and those under conditions of confinement have implications for a vast array of human situations. The effects of life in the wild are not necessarily "good" and the effects of

life in relatively confined circumstances are not necessarily "bad" for either man or animal. Protection of an endangered species takes precedence over the view that the natural way is best:

> Preservation by domestication in an alien environment is far better than extinction in the natural habitat (Bertram, 1969).

Lest the social atmosphere become too rarified, it is a thoughtful reminder to note:

> All these experiments have convincingly shown that when populations of a number of species are subjected constantly to certain artificial conditions that appear to favor growth and survival of individuals, the result is not only the death of many individuals, but after a time, the extinction of the race (Spencer, 1958).

The more specific matter of the effects of bringing many individuals together over relatively long periods of time, whether in the wild or in captivity, can and should be studied in detail. One outcome that has been discovered in species as far removed as crocodiles, trout, and man is the phenomenon of social distancing. A distance order in which individuals space themselves out in a uniform way under population crowding applies to all those species who have territorial behavior, dominance orders, and personal space requirements. We do not yet know the critical point in the formation of these social behaviors, what functions are served, or what conditions lead to which social form. We are particularly ignorant about the spatial needs of primate groups, human and otherwise, who cannot so quickly and easily be studied over several generations as can the white rat.

One speculation is that reduction in physical space results

in social spacing and distance orders. Another speculation based on a good deal of observation is that either limited space or increased population density leads to increased aggressive behavior (Hediger, 1964). In nonhuman primates aggressive interactions increase at feeding time when several animals are congregated in a small area whether in the wild or in semi-captive conditions (Goodall, 1965; Hall, 1963; Jay, 1965; Southwick, et. al, 1965; Wilson and Wilson, 1968; Zuckerman, 1932). It is tempting to infer a strong positive correlation between crowding, aggression, and dominance hierarchies. Scott (1958) pointed out that any group of animals that can fight can set up a dominance order. He also stated:

> Unlike most types of social organization, which tend to weaken and disappear in captive animals, dominance relationships in captivity can be strengthened or even created where none existed before.

The social interactions of the Japanese monkey indicate similar complimentary relationships between group size, space, aggression, and social organization:

> If the population is unusually large, as in the Takasakiyama troop the tension among individuals also increases, making social organization naturally firm and the inhibition of a troop upon individuals powerful (Itani, 1958).

In certain fish, bird, and rodent populations high densities produce a shift from the holding of territories to the maintenance of individual dominance (Marler, 1956). In canaries, confinement in relatively small space results in a social order which is more simple and more definite and in which there are no complications

over territorial rights. With greater space, individual territories become established in which each bird is supreme regardless of his dominance rank in neutral ground (Shoemaker, 1939). Both natural and experimental behavior indicate greater amounts of fighting and tension around competitive situations in which something is limited in supply, and the ultimate significance of crowding and spatial factors may be in the area of supply and demand.

Turning more specifically to human and nonhuman primates, most of the observations of dominance behavior have been made under competitive foodgetting situations (Altmann, 1968). How representative such competition is of "social behavior" in general has been questioned, (Altmann). One study indicated, for instance, that the correlation between success in a food situation and other kinds of agonistic behavior in monkeys was low (Warren and Maroney, 1958). Greater clarity about relationships between dominance interactions of different sorts, and between dominance and amount of fighting in primates is sorely needed. The relationship between social facilitation under a dominance hierarchy as compared to another type of social organization also needs clarification.

Yerkes (1943) refuted the concept of equality of ability or of opportunity in a group of captive chimpanzees. He stated that what the individual chimpanzee may do and what is expected of it depend in the first place on its ability to achieve and defend social status in the dominance hierarchy. He found that the aggressive seeking of a higher position was one of the basic principles of the chimpanzee social structure in captive chimpanzees.

One aspect to captivity which can be a catalyst to destructive aggression is the distortion of normal male-female ratios. Zuckermann gave an account he witnessed in the London Zoo among hamadryas baboons who were severely disproportionate in relative number of males:

> The fight lasted for several days, and after the female was killed, 24 hours passed before the body could be removed from the Hill. During this interval fights continued to rage around the body, which changed hands several times. Its owners carried it around by the waist, groomed it, examined its ano-genital area, and often copulated with it.

Contrasting aggressive behavior between free-living and confined laboratory-born rhesus monkeys, Mason (1960) found that the frequency of aggressive behavior for a feral versus a restricted (removed from the species at birth) group was significantly higher for the latter. Aggressive episodes tended to be longer in the restricted monkeys. These animals had a tendency to react with aggression when attacked, whereas the feral subjects generally withdrew from attack or else submitted passively and without retaliation.

Noting that almost nothing has been published on the nature of aggressive behavior of chimpanzees, Wilson and Wilson (1968) described and defined the behavior observed in a group of chimpanzees living in a semi-free-ranging environment. It was observed that aggression was much more common in this captive situation than in the natural habitat. It has been reported that certain animals had a higher status than other animals as a consequence of large size, sex, (males over females), and estrus.

The social behavior and social structure of Japanese macaques in confinement were studied by Alexander and Bowers (1967). Substantial deviations were noted between the spatial structure of the confined Oregon troop and the central-peripheral structure typical of free-ranging troops in Japan. There was also some indication of heightened aggressiveness within the troop.

Similarly, Kawai and Yoshiba (1967) reported that when a troop of Japanese monkeys were transplanted to a small islet, there was an increase in the frequency of agonistic behavior "due to a limitation of the troop range."

Whereas chimpanzees living in the wild do not seem to form a dominance hierarchy but instead appear to live in very loosely organized aggregates with a minimal number of dominance interactions and little aggressive behavior (Goodall, 1965; Jay, 1966; Reynolds, 1965), recent findings indicate that space available in a food-competition situation in captivity may be an important variable in producing a dominance hierarchy kind of social structure. Thus chimpanzees in captivity were observed to form a dominance hierarchy which was altered as physical space increased (Hodan, 1970; Pearce, 1970).

At the human level the effects of restricted space and/or relative crowding on the social behavior of children, such as those raised in institutional settings, may result in a much more narrow range of interpersonal behaviors and adaptability to other people (Bowlby; Spitz). Adults in confinement have been observed to establish personal "territories" as well as definite "peck

orders" as a means of adjustment (Sommer, 1969). On the basis of aggressive acts between mental patients, it was evident that a relatively stable "dominance hierarchy" existed (Esser, 1965).

Goffman (1961) pointed out his observations of life in a mental institution:

> I have mentioned two kinds of places over which the patient has unusual control: free places and group territories. He shares the first with any patient and the second with a selected few. There remains private claim on space, where the individual develops some comforts, control, and tacit rights that he shares with no other patients except by his own invitation. I shall speak here of <u>personal territory</u>.

He goes on to point out another observed feature of adjustment to life on the ward:

> ...on the bad wards, a special pecking order of a sort occurred, with vocal patients in good contact taking favorite chairs and benches from those not in contact.

The social mechanisms employed under circumstances of confinement and close contact with many people may well represent the individual's attempt to deal with behavior, relationships, or emotional outlets that are overly stressful (Hall, 1966).

Recent Research on Dominance Hierarchies

Monkeys and apes living in the wild almost all live in social groups consisting of males and females of all ages. These groups may be relatively open to additional animals in some instances and relatively closed in others (Washburn and Hamburg, 1965). Within the larger primate group there are several subgroup relationships which are more or less of long standing and mutual

influence. These relationships include the mother-infant, the mating, and various coalition subgroupings. Particular kinds of learning accrue from each type of association and, in the case of dominance interactions to be discussed shortly, certain power advantages can result. Another advantage of long-time association among members of the larger social group comes from each member knowing all the other members well. Within a particular social environment of familiar animals, an important feature of life is the high degree of predictability of behavior which is assumed to exist (Schrier, Harlow, Jay, 1965).

One common feature of the social organization of all non-human primate groups is the dominance structure, however formed and however stable. During the course of daily activities of a troop or aggregate, individuals will come into contact in situations involving competition of some sort, and the "issue" will be settled through an encounter in which one will come out on top. In time a series of conventions or communicatory behavior will substitute for open hostility or open aggression, so that in any encounter it will be relatively clear who is expected to win and who is expected to lose or step aside. The total social structure of the group with regard to situationally predictable outcomes of dominance interactions is the dominance hierarchy of that group. The forms of dominance hierarchies are variable, and all change under certain circumstances. The importance to the individual of his particular position in the hierarchy is that his relationships with other group members are in large part mediated by his status

position in relationship to theirs. It is usually assumed by human observers that the dominance order of a group is especially important in maintaining the social cohesiveness and consequently the social adaptiveness of the society. Without the group most primate individuals would not long survive.

Briefly, the factors which seem to determine relatively higher dominance status pertain to those personal characteristics which give one individual the "edge" over another: size, strength, sex, cleverness, state of estrus, boldness, confidence, etc. The stability or even rigidity of a nonhuman primate groups' dominance structure depends upon factors which are poorly understood. In other words, the fact that langurs of northern India form a stable male dominance hierarchy (Shrier, Harlow, Jay, 1965) and that chimpanzees in the wild do not cannot be clearly attributed to any social or environmental factor at the present time. The usual ad hoc explanation of dominance structures is that they are intimately related to the groups' aggressiveness and serve as a means of tempering aggressive interactions. If this is true, then it should be possible to correlate "natural" aggressiveness with tightness of social structure in some way. In dogs, Scott found that there was a greater tendency for more aggressive breeds to develop a straight-line dominance hierarchy with each animal dominant over those in the lower ranks (Scott and Fuller, 1965). However, in shelties a dominance order based on space seemed to indicate that differences in dominance hierarchies may be developed in specific kinds of situations. Normal infant rhesus form firm

dominance relations through their aggressive encounters, and status positions among both males and females tend to remain stable for long periods of time (Harlow and Harlow, 1966). A factor perhaps making for differences in dominance stability may be that of ability to utilize subtle gestures in dominance interactions (Jay, 1966). In chimpanzees, dominance interactions reportedly constitute only a minute part of behavior in the wild. Neither male nor female individuals show a clear dominance hierarchy, although males seem to be dominant over females (Jay, 1966). An important but often neglected matter in the determination of dominance relations is the matter of coalitions forming as a subgroup of the whole social structure. Such coalition behavior appears to play a vital role in the stability of the dominance hierarchy (Alexander and Bowers, 1967; Hodan, 1970; Jay, 1966; Kawai, 1965; Kawamura, 1958).

Stress, Dominance Status, Individuality

The concepts so far discussed all have a bearing on individual requirements for space. Territories, dominance hierarchies, status systems, and personal space are all mechanisms which produce spacing among social individuals. At the Hominoid level the greater individual complexity which exists is reflected in the greater social complexity which must be developed to take care of social spacing. The personal space requirements for such individually complex primates as chimpanzees and human beings have to be suitable for the mediation of all kinds of involved personal

transactions. The complexity of individuality among humans and chimpanzees may well be the most salient characteristic of these two groups. The level of individuality attained comes out of the degree of differentiation possible in the psychological and social development of animals, and in fact "individuality" and "differentiation" are synonymous terms. A well differentiated individual is one who maintains clear individual boundaries between himself and others, and a concept of the importance of individual boundaries plays a major role in psychological and sociological theory (Erikson, 1956; Hall, 1969; Miller, 1962; Sommer, 1969). A breakdown of individual boundaries is often seen in terms of "mental illness," social chaos, and destruction of cultural values. A certain degree of separateness is apparently required for the orderly regulation of interpersonal and intergroup behavior. As larger numbers of individuals come into closer proximity with less space, the liklihood of greater social stress and a collapse of normal individual boundaries becomes very possible.

Coalitions and Stability of Dominance Hierarchies

Several investigators have referred to the importance of certain alliances upon the social ranking systems of primate groups. Coalitions formed by two or more animals working together with an increased power base may be referred to by such names as "friendships," "subgroups," "central hierarchy," "dependent ranks," etc. The individual animals in the coalition are able to achieve some social advantage through uniting in certain situations. The social

position of a monkey may be raised, for instance, through its association with a relatively high-ranking member. An extention of social prestige or power through coalition-formation has been observed in situations involving aggressive threat, fearful reactions, and various types of competition. Kawai (1958) introduced the important concepts of 'basic rank' and 'dependent rank' in describing dominance behavior. Thus the basic rank of an individual is seen as his social rank in simple interaction with another individual, and dependent rank is defined in terms of the special influence the individual carries as a result of his relationship with a higher ranking individual. Basic rank comes about as a result of what the animal can do on his own, and dependent rank through some degree of "power by association." For example, a subadult male may have a different rank among its peers depending upon the presence or absence of its mother. Or a young adult male may have different rank depending upon the proximity of higher ranking males and upon his relationship to them. Jay said:

> It is evident from field studies that the presence of other individuals may influence status and status in association with others.

In a recent study by Hodan (1970) with captive chimpanzees, the presence of a linear dominance hierarchy was discovered in a one-cage situation of the food competition type. Following determination of the dominance hierarchy which emerged from the results of all possible dyads among a group of pre-adolescent chimpanzees, an investigation of coalitions in triadic groups was carried out. Based upon a theory of coalition behavior in humans in triadic

situations (Caplow, 1956; 1959; Gamson, 1961), Hodan predicted the formation and the success of coalitions when three animals were placed together in a competitive situation. Two kinds of coalitions, "overt" and "covert" were defined and tested separately. Using a one-cage and a two-cage situation, two subjects were observed to unite openly and aggressively against a third in 16 out of a possible 420 trials. In only one of the 16 coalitions did the two subordinate S's form the coalition as predicted, the most frequent coalition being formed of the S's with highest and lowest status. In 14 out of the 16 instances, the highest and lowest status animals united against the middle status animal and out of these five coalitions were successful as defined. Significance of predictability of coalition behavior in the triad on the basis of the linear dominance hierarchy was found at $p \leq .05$. It was found also that whereas effective covert (statistical) coalitions increased when space was increased, overt (open attack) coalitions decreased to almost non-existence.

An investigation of the effects of space, estrus, and coalitions on the dominance hierarchy of a group of mature chimpanzees was carried out very recently by Pearce (1970). These four animals were used to investigate coalitions in the triad and to extend the testing of the theory to the tetrad if possible. As with Hodan's study, only observed overt coalitions were accepted. The results failed to support any of the existing theories of coalition formation in contrast to Hodan's findings. Two overt coalitions in the one-cage and one in the two-cage situation were

observed and were not statistically significant. It was concluded that insufficient data on coalitions in these older animals was the case.

In human societies there are many instances of coalition behavior in which minority groups align against the major power, minority groups unite in rebellion against established authority, and coalitions form as pressure groups so that their voices may be heard. As with nonhuman primate groups, human coalitions can be seen against a context of relatively stable or nonstable status systems. The amount of conflict presented by a coalition against another individual or coalition of individuals will obviously depend upon whether there is competition for power over a long period of time. When things are "settled" between conflicting factions, as in labor disputes, treaties, court decisions, or the triumph of one group over its enemy through winning a fight, further competition ceases. Apparently the type of power structure or organization in part determines the necessity or desirability of coalition development. Sociological theories such as Caplow's and Gamson's do not seem to be particularly concerned with the specifics of overall organizational structures. Dalton (1959) studied rule-breaking of a systematic sort among employees of industrial firms, department stores, and other businesses. He found that continuing "rebellion" of this sort was probably the result of a tacit and informal approval of appropriation of materials and services (Dalton, 1959). Another study revealed that

in a similar situation one group will not "blow the whistle" on another if they are partners in a system characterized by a balance of power and interest (Becker, Howard S. Outsiders. p. 126). In other words, it would seem very likely that the formation and the success of coalition behavior within a social organization has to do with the whole matter of "law enforcement." Whatever the specific situation, coalition behavior would seem to be most properly seen in terms of the relationship of the coalition to the total structure. Sociologists make a distinction between those features of society which promote stability and are called "functional," and those which disrupt stability and are thus "dysfunctional."

In nonhuman primate groups, a breakdown of the normal social structure in captive Japanese monkeys resulted in much more aggressive behavior in the form of "mobbing" and "shifting troop attack," both of which consisted of coalitions which ganged up to attack another animal. Instead of the concentric rings of diminishing dominance found in the wild, one undisputed leader and relative looseness of structure in the rest of the troop emerged with a group of males perpetually afraid and subordinate to all other members of the group (Alexander and Bowers, 1967). Some studies have shown that the role of the dominant males in monkey groups is to mediate aggressive behavior within the group (Tokuda, Jensen, 1968). It can be assumed that individual differences in leadership or dominance will therefore be transferred to intra-group aggression, whether from coalitions or from individuals. To

date no experimental studies have provided data on the possibility that the existence or nonexistence, and the success or failure, of coalitions may depend upon the amount of power or dominance of the leader. Some indirect evidence exists that the role of the most dominant male includes breaking up fights, stopping a chase, controlling an attack, etc. In fact, it was found that when the leader male was out of the group there were significantly more aggressive episodes, and when he returned to the group the number of aggressive episodes returned to normal (Tokuda, 1968). Alexander and Bowers (1967) speculated that the deterioration in troop organization observed may have been the result of the inability of the troop leader to initiate and guide troop movements as he could in the wild. This possibility plus the monotony of the monkey's environment were probably important in the increased aggressiveness among corral Japanese monkeys.

It may well be that coalitions, like other forms of rebellion against the normally most powerful individuals, can be related to the sureness and consistency of the "leaders" rather than to other factors such as additive strength or "gamesmanship" of the members of the coalition. The leadership qualities of an individual man or chimpanzee might well be thought of in terms of amount of personal space which surrounds them in a situation in relation to the personal space of the other individuals. An individual with more personal space would be someone with more confidence and a clearer notion of his role in relation to others. He would probably be characterized by less overt aggression as a general

rule because he would find few instances in which retaliation or defense are necessary. A theory of coalitions based on group stability versus instability might be indicated.

CHAPTER II

STATEMENT OF THE PROBLEM

The present study was designed to investigate the interpersonal behaviors and social organization of captive chimpanzees in relation to changes in group size, space, and coalitions. Previous studies on social organization in captive chimpanzees (Hodan, 1970; Pearce, 1970) showed that chimpanzees placed in a competitive situation with relatively little space will form a linear dominance hierarchy when either dyads or triads are used to define the hierarchy. When the space was increased, both studies found that most of the animals in the dominance hierarchy either changed position or moved closer together in ranking. In Hodan's results, only the Alpha and Beta animals retained significant distances from the others when run in two-cage triads. The rest of the subjects were for all intents and purposes not clearly differentiated from those below and those above them in the hierarchy. In Pearce's study, using four mature chimpanzees, all hierarchical positions shifted in the two-cage situation. The data on the effect of coalitions on the social structure seemed contradictory in the two studies. Whereas one study found that coalitions could be predicted from coalition theory in humans (Caplow, 1956; 1959; Gamson, 1961) the other study found no support for these or any other theory of coalition behavior now

in existence. The difference in results on coalitions in the two investigations may well reflect differences in age and/or familiarity of the animals with each other. Hodan's subjects were adolescent and preadolescent chimpanzees who had been in the colony for different lengths of time, whereas Pearce's subjects were four adult chimpanzees who had lived closely together for many years. Also, there is some evidence (Wilson and Wilson, 1968) that younger chimpanzees may engage in more open aggression than older, more socially stable animals. With regard to the composition of overt coalitions which attacked a third animal, Hodan found that in almost every instance the coalition was formed by the top animal and the bottom animal in the triad. These two would attack the middle animal who was the one "challenging" the dominant chimpanzee for food or status. The question was raised whether it could be said that coalitions in chimpanzees consist of the top-ranking and bottom-ranking against the middle, or whether it is the top animal plus the lower animals against the animal second in line or dominance. In other words, when coalitions are formed what function do they serve? Is it a matter of ganging up on a challenger because of some kind of "allegiance" to the leader? Is it a matter of attacking an animal who is behaving inappropriately? Is it a way to increase the rewards of the lower-ranking animals through joining forces?

The data to the present time indicate that chimpanzees confined to a small space behave differently in certain ways from chimpanzees in their natural habitat (Hodan, Pearce, Wilson and Wilson, Yerkes). First of all, the results of competitive dyads and triads

indicate that a linear dominance hierarchy may emerge. Second, several studies of chimpanzees in confinement show a much greater proportion of aggressive behavior than is reported in the wild. The previous studies do not, however, provide enough information to show whether it is the effects of crowding or the effects of space alone which produce differences in social behavior. The traditional experimental manner of defining a dominance hierarchy is to rank all the animals according to the number of food units they each obtain in the dyadic situation. A much more pertinent way to determine the presence or absence of a dominance hierarchy would be to test for it directly. That is, since an animal's position in the hierarchy supposedly represents dominance over all lower ranking animals it should be possible to verify this by actual test. Consequently in the present investigation each chimpanzee was given his position or rank order if he was shown to be significantly dominant over all subordinate chimpanzees when they were all tested together. Based on the original hierarchy formed from dyads in the one-cage situation, it was predicted that certain individuals would be overwhelmed or outmaneuvered when they had to compete with all the animals subordinate to them. This prediction was made on the assumption that either smaller or more inconsistent distances between animals would result in loss of dominance position under conditions of crowding. It was also hoped that male-female differences would be more apparent in the present study because of two additional males placed with the original group used by Rowdan. It was assumed that the effects of

crowding would be observable as the space variable was held constant, and that the effects of space could be observed as numbers of individuals was controlled.

Using a direct test of dominance under restricted space, the following hypotheses were formulated for the first part of the study.

Hypothesis I. The social structure of captive chimpanzees is organized around a linear dominance hierarchy which includes both males and females.

Hypothesis II. The linear dominance hierarchy is not as apparent when the number of individuals is increased to include all animals subordinate to each individual animal.

Hypothesis III. Changes in the linear dominance hierarchy will take place at the "weakest points" under crowding i.e., those points at which animals are either not spaced at significant social distances or at which there is variability in spacing between adjacent individuals.

Hypothesis IV. Changes in the linear dominance hierarchy as a result of crowding will occur between females.

Hypothesis V. Stability of dominance position will most often be true for males.

The second area of investigation concerns the effect of crowding and space on aggressive behaviors. Two classes of agressive behavior were selected for observation: behavior in overt coalitions as defined previously and individual aggressive behavior. Earlier primate studies indicated that both crowding and restricted space result in increased aggression. (Alexander and

Bowers; Southwick; Wilson and Wilson) It was therefore predicted that aggression would increase as group size increased. Overt coalitions were predicted on the basis of original power of each individual in the original hierarchy. The following hypotheses for the second part of the study were formulated as stated:

Hypothesis VI. Coalitions will most often consist of the dominant animal and the subordinate animals against middle animals who "challenge."

Hypothesis VII. As the number of individuals increases the frequency of coalition behavior will increase.

Hypothesis VIII. As the number of individuals increases the frequency of individual aggression will increase.

The third and last part of the experiment was to investigate the effects of increased space on the linear dominance hierarchy if a linear hierarchy emerged in part one. The hypotheses formulated were these:

Hypothesis IX. The linear dominance hierarchy is not as apparent when space is increased, i.e. individual distances will become smaller.

Hypothesis X. The linear dominance hierarchy will change most often at those points between adjacent females.

Hypothesis XI. Stability of hierarchical position will most often be true for males.

Hypothesis XII. Coalitions will most often consist of the dominant animal and the subordinate animals against middle animals who challenge.

Hypothesis XIII. As the amount of space increases the number of coalitions will decrease.

Hypothesis XIV. As the amount of space increases, the frequency of individual aggression will decrease.

It was expected that if the factors of increased numbers and decreased space are essentially the same then no significant differences in their effects would be found.

CHAPTER III

METHOD

Subjects

The subjects which took part in this investigation consisted of the seven chimpanzees used earlier by Hodan in his recent study, (1970) plus two additional males: one adolescent male (Se) and one adult male (Mu) previously used by Pearce (1970). The subjects thus included a total of nine chimpanzees, four of which were males ranging in age from preadolescent to adult. The five females included individuals ranging in age from about seven years to 12 years at the time of the study. The males ranged from at least 7 to at least 20 years of age. The two males Mu and Se were both collected by one year and human reared, although Mu spent many years in a zoo with three female chimpanzees and Se was reared in a completely human environment. Both of these males were atypical; their behavior will be described in some detail later. The other two males, P and Me, were both born and captured in the wild when each was approximately one year of age although the behavioral differences between the two were vast. Whereas P proved to be extremely dominant for his age, and sexually quite advanced, Me was usually unable to maintain dominance with even

the youngest and smallest female. He usually elicited much aggression from the other animals against him, and he exhibited a good deal of apparent frustration when he couldn't obtain food rewards. He was, however, sexually accepted by various females in the group. A wide variety of personal characteristics also was true of the females. The oldest female, Mo, had been raised to perform in show business and had learned many tricks. Another female, We, was born and captured in the wild along with the male, P, and she seemed the most unpredictable in behavior of all the subjects. The two females Ca and Mi were acquired together when about one year old, although Mi received more human contact because she was more responsive to them. Pe was acquired from a family in Africa. She was described as shy with humans, but as persistent and wiley when in competition with other chimpanzees (Hodan, 1970).

Experimental Design

Apparatus. The apparatus used consisted of three major units: A Coin Receiver-Ejector Unit (CREU); the Feeder; and a Switching Unit-Remote (SUR). The CREU was mounted in an upright plywood enclosure measuring 48" x 40" x 20" and contained a nickle coin ejector, Gerbrands Model B; a 28 volt, direct current, 4 amp power supply; an automatic switching unit; an annunciator; and a coin receiver modified to accomodate wet nickels.

The Feeder portion of the apparatus was a Davis Universal Feeder, Model 320. The SUR was composed of four non-locking push-button switches and a ready light which indicated to the operator

the readiness of the system for another cycle. The four switches performed the following functions: the first switch initiated the cycle; the second switch effected a coin without the annunciator in the event that the effector failed to function properly; the third switch operated the Feeder in the event of malfunction in the coin receiver which would result in failure of the automatic Feeder; and the fourth switch served the function of clearing the coin receiver in the event a coin happened to lodge at some point in the coin receiver while in transit (Hodan, 1970). Schematics for the entire apparatus appear in the Appendices.

Two cages (C1 and C2) were located adjacent to each other and comprised the two test cages. These cages were part of the normal living area of these chimpanzees and the only transportation involved in the experiment was movement from one cage to another. The cages were identical in size with the dimensions 8'9" x 10'4" x 7'. Grapes were used as rewards and the feeding of the animals was arranged so that they were fed at least four hours prior to the beginning of each series of trials. This feeding schedule eliminated the possibility of satiated animals being used in the experiment, and as a matter of fact the chimpanzees always seemed hungry for grapes during the experimental procedures.

The CREU was affixed permanently to the side of C1 and the Feeder was mounted on a plywood platform and was suspended from the ceiling. Provisions were made so that the Feeder could be moved from atop C1 to C2 whenever necessary for experimental purposes. A metal plate with a coin slot was welded to the inside of C1 where the CREU was affixed to receive the coins.

Procedure. All nine chimpanzees used in this investigation had previously undergone shaping procedures to operate the apparatus. All but one had also taken part in a previous study so that the experimental experiences were essentially the same for all subjects. In order to make a systematic check of the assumption that all the animals were equally prepared to perform the experimental task it was decided to test each animal's ability to operate the apparatus in comparison to the others. The method of checking initial equality of performance was arbitrarily determined by each chimpanzee's ability to complete a series of experimental sequences within an arbitrary time-limit. To reach the criterion expected, each animal had to be able and willing to take the nickel from the coin container following the buzzer, to place the nickel in the slot entering into the coin receiver, and to retrieve and eat the grape which was subsequently ejected through a hole in the top of the cage. The whole sequence was to take place without significant delay so that it could be determined whether the subject was aware of the connection between buzzer and ejection of nickel into the cup, between placing the nickel in the slot and the working of the mechanism which produced grapes, and so it could be determined that grapes were equally appealing to all subjects. When each subject had demonstrated that he could go through the whole sequence ten times in rapid succession with an interval no longer than five seconds between buzzer and retrieving the coin, and an interval of less than ten seconds for the entire sequence, it was then assumed he had "learned" the

experimental manipulations to an acceptable level. All the animals met the criterion set up, although additional shaping procedures for the two new males and for the lowest ranking male in the previous study, Me, were found necessary in order to bring them to a comparable performance level with the other animals.

The next step was the introduction of Se into the colony, since up to that time he had been separately caged and had not previously taken part in a dominance experiment. For one week Se lived with and became known to the other members of the colony before he was introduced to the experiment. Upon his entering the colony, much aggression toward him was observed, especially aggression from P who is usually a very dominant young male within the daily activities of the group. P attacked Se a few times and so did some of the females, so that Se would not come down off a shelf to join the others for 2 or 3 days. Eventually Se and P seemed to get something "settled" and they were frequently observed sitting together on a shelf, grooming each other. Se was also observed sitting with the largest females toward the end of the week.

Se was officially entered into the experimental situation by placing him in competition with each other individual in all possible dyads just as the other subjects were in the previous experiment (Hodan, 1970). Only a few weeks between Hodan's study and the present one had elapsed so that it was assumed that the relative dominance positions of the animals was the same as observed

in his study. This assumption was verified by observations of other behavior during the daily activities of the colony. Se's relative position in the group on the basis of dyads was thus determined as it had been for the others.

It was originally planned to enter the other new male, Mu, in the same fashion that Se had been introduced. However shortly after Mu was placed with the rest of the colony he became involved in a fight during which he was severely lacerated. While his wounds were mending, and since Mu was atypical in being the only fully adult chimpanzee, it was decided to test Mu separately and not as a part of the main body of the experiment. His behavior with the others and their behavior in relation to him are thus observed and reported apart from the other results. It was therefore possible to discover the individual effects of each additional male one at a time on the hierarchical behavior within the colony.

In order to test the hypotheses of the first part of the study, the direct-testing method for a linear dominance hierarchy took place as follows: all eight chimpanzees were tested in the food-competition situation to see if one animal would emerge as significantly dominant. If so, he was removed and the rest of the group were then tested in the situation. If an animal proved to be significantly dominant in this situation he or she was removed and the remainder tested together, etc. This procedure was used until the bottom of the hierarchy was reached except when no dominant chimpanzee emerged from a group. In this event, the animal expected to be dominant on the basis of the original hierarchy in

Hodan's study was studied further in relation to his "subgroup." What seemed to be the cause of the shift in dominance? Was the animal overthrown by a certain number of subordinates? Was it a coalition which was responsible? Was it a particular individual? Suppose for instance that the expected Beta animal did not obtain a significant proportion of grapes in competing against all six chimps "below." The next experimental step would be to place this subject in competition with all combinations of five, and then against all combinations of four, etc. until the point was reached at which clear dominance in the situation was demonstrated. This procedure turns out to be a study of numbers, individual leadership, individual challenges, and coalitions within the entire group. It was hoped that the particular mechanisms operant in coalitions would be apparent from these procedures. The systematic reduction of numbers of individuals present in groups, with space held constant, made the effects of numbers alone apparent. A much clearer notion of the nature of the linear dominance hierarchy was expected to come out of the design, particularly the nature of changes within the hierarchy.

The tabulation of coalitions was on the basis of either overt or covert coalitions, although only overt coalitions were tested in the hypotheses. These are defined as in Hodan's study as only those instances in which two or more animals unite to attack another individual.

The tabulation of individual agonistic behaviors is on the basis of the behavioral taxonomies presented on two different

captive populations in two different studies (Hodan, 1970; Wilson and Wilson, 1968). These taxonomies present the most complete catalogue of aggressive-submissive behaviors in captive chimpanzees known to the present investigator at the present time.

The two-cage situation was a replication of the one-cage study with the additional factor of increased space. In order to obtain a grape, the dominant animal (or other animal) had to place a nickel in the slot in one cage and then run to the grape dispenser in the second cage via a third cage. The variable of increased space created a strain on one animal's ability to maintain his or her influence over the group, and provided ample opportunity for increased attempts by subordinate chimpanzees to get a grape.

The number of grapes obtained is the dependent variable throughout the experiment. All sessions consisted of 12 trials each, and no evidence was found that the subjects became satiated with grapes at any time during the entire study.

CHAPTER IV

RESULTS

The presence or absence and the type of dominance hierarchy for the first part of the study were determined by the number of grapes each animal received under the experimental conditions. Although behavior related to placing coins in the coin receiver was also observed and recorded, this behavior did not enter into the statistical results. The statistic chi-square (Walker and Lev, 1953, p. 86) was used to determine whether the number of grapes obtained by any one individual in a group was significantly different from that which could be expected on the basis of chance alone. The chi-square statistic was thus specially adapted as a means of determining significant "individual differences" between a subject and the rest of the group. These differences or distances were compared to those previously established in the original hierarchy established through dyads and triads (Hodan, 1970). It was assumed in the present study that the dominance hierarchy originally based on triads would be a closer approximation than that based on dyads to results with increased numbers beyond the triad (tetrads, groups of five, six, seven, eight, and nine).

Overt and covert coalitions were predicted on the basis

Table 1

Chi-square Values for Triads in the One Cage Condition (from Hodan)

Critical Values

$x^2 = 12.00, p \leq .001$; $x^2 = 8.32, p \leq .005$; $x^2 = 5.32, p \leq .025$; $x^2 = 3.00, p \leq .10$

	W/Mo	W/Mi	W/Pe	W/Ca	W/Me	Mo/Mi	Mo/Pe	Mo/Ca	Mo/Me	Mi/Pe	Mi/Ca
P	12.00	12.00	12.00	12.00	5.32	12.00	.32+	12.00	12.00	12.00	12.00
W						12.00+	12.00+	12.00+	3.00+	5.32	5.32
Mo										12.00	8.32
Mi											
Pe											

Note. A + sign following a chi-square value indicates an effective coalition.

Table 1 (continued)

Chi-square Values for Triads in the One Cage Condition (from Hodan)

Critical Values

$x^2 = 12.00, p \leq .001$; $x^2 = 8.32, p \leq .005$; $x^2 = 5.32, p \leq .025$; $x^2 = 3.00, p \leq .10$

	Mi/Me	Pe/Ca	Pe/Me	Ca/Me
P	12.00	12.00	12.00	12.00
W	8.32	12.00	8.32	5.32
Mo	5.32	8.32	3.00	12.00
Mi		1.32+	12.00	5.32
Pe				.32+

Note. A + sign following a chi-square value indivates an effective coalition.

of the original power demonstrated by each subject in the dominance hierarchy obtained in the one cage situation. The number of grapes acquired by a previously established dominant member and by the previously established subordinate members were compared to the number that would be expected purely on the basis of chance. Since the earlier results showed essentially the same hierarchy for both dyads and triads in the one cage condition, mention of the "original hierarchy" refers to results in the triad unless specifically stated otherwise. In other words, the triadic hierarchy will be used for predictions in the present study with the implicit understanding that only minor shifts occurred in the dyadic hierarchy, and that these shifts were not statistically significant.

An effective coalition was operationally defined as a situation wherein 1) the combined number of grapes acquired by two or more subdominant members of a group was significantly greater than that which could be expected purely on the basis of chance. or 2) the number of grapes acquired by the dominant member of the group and the combined number of grapes acquired by the subdominant members of the group did not differ significantly from that which could be expected on the basis of chance alone. The alpha level chosen for all statistical analyses was $p \leq .10$ as a means of maximizing the opportunity to discover all differences which might be present. The number of degrees of freedom of each x^2 test was n-1 where n equals the number of categories.

The first hypothesis tested was the social structure of captive chimpanzees is organized around a linear dominance hierarchy including both males and females when a direct method of testing

is used. The effects of space and also the effects of estrus were controlled by confining the subjects to one cage and by comparing differences in behavior during maximal perineal swelling for two females, Mo and W. Differences in hierarchical behavior between females or between females and males as a function of estrus were controlled since it has been shown that this factor enters into changes in female dominance, (Hodan, 1970). It was found that during the course of the present investigation changes in estrus as measured daily by amount of perineal swelling did not result in significant differences in the relative dominance positions of females. The chi-square values for all size groups in the one cage condition are presented in Table 2. Examination of the results in Table 2 shows that there are just two exceptions to a completely transitive, linear dominance hierarchy. On the basis of a simple majority of the grapes obtained by each animal there is only one exception to a completely linear dominance hierarchy. It was concluded that the deviation from a straight-line dominance hierarchy produced by the direct-testing method was minimal and the null form of Hypothesis I was accepted.

The second hypothesis asserts that the linear dominance hierarchy formed when the number of individuals is increased to include all subordinate animals will be distinct from that based on triads. A comparison of the rank order of the subjects based on these two different approaches appears in Table 3. It can be seen that the order remains the same with just one exception: two subjects were equal in the number of grapes each obtained in the

Table 2

Chi-square Values for All Groups in the One Cage Condition

Critical Values

$x^2 = 12.00, p \leq .001$; $x^2 = 8.33$, $p \leq .005$; $x^2 = 5.33, p \leq .025$; $x^2 = 3.00, p \leq .10$

	Mo W Mi Se Pe Ca Me	W Mi Se Pe Ca Me	Mi Se Pe Ca Me	W Se Pe Ca Me	Se Pe Ca Me	Se Pe Ca Me	Pe Ca Me	Ca Me	Ca	Me
P	12.00									
Mo		12.00								
W			0+ ++		12.00					
Mi				0+ ++		12.00				
Se							8.33			
Pe								1.33+	1.33	12.00
Ca										12.00
Me										

Note. A + sign following a chi-square value indicates an effective coalition.
A ++ sign following a chi-square value indicates an overt coalition.

Table 3

Comparison of Dominance Hierarchies in the One Cage Condition When Triads are Compared to Complete Dominant-Subordinate Groups. Hierarchy (2) has One Additional Male Subject.

(1) Dominance Hierarchy in the One Cage Condition (Hodan)	(2) Dominance Hierarchy in the One Cage Condition (King)
*P	*P
*Mo	*Mo
*W	W-Mi (equal)
Mi	*Se
Pe	Pe
Ca	*Ca
Me	Me

Comparison of Dominance Hierarchies in the Two Cage Condition When Triads are Compared to All Dominant-Subordinate Groups. Hierarchy (4) Includes One Additional Male Subject.

(3) Dominance Hierarchy in the Two Cage Condition (Hodan)	(4) Dominance Hierarchy in the Two Cage Condition (King)
*P	*P
Mo	Mo-W (equal)
Mi	*Mi
*W	*Ca
Ca	*Pe
Pe	*Se
Me	Me

Note. The Hierarchies from Hodan's study are those based on Triads. An * sign preceding the subject indicates significant individual distance between the subject and all those below.

one cage condition. It was assumed that this one exception did not represent a significant change in the overall structure of the linear dominance hierarchy and the hypothesis was rejected.

The third hypothesis tested was that any changes which do occur in the linear dominance hierarchy will take place at the "weakest points," i.e., those points at which subjects are not spaced at significant distances or at which there was variability in spacing between adjacent individuals. Comparison of the two hierarchies reveals that shifts occurred at points where adjacent subjects were not separated by significant individual distances in the triad. These shifts were predicted on the basis of inspection of Hodan's chi-square values (see Table 1) showing that W and Pe did not maintain significant dominance in the triad. All had successful coalitions against them and therefore were expected to be even less able to maintain dominance position under greater "pressure" of increased numbers. Since the Alpha animal, P, maintained significant dominance in 14 out of 15 encounters and his one "upset" was shown to be related to estrus in the top ranking female, it was predicted that his position would be maintained. Table 2 reveals that all predictions were supported by the data and the hypothesis was accepted.

Hypothesis IV states that changes will occur most often between females when number of individuals is increased within a relatively small space. Comparison between results in the triad and results in complete dominant-subordinate groups shows that the only changes in the hierarchy were those involving females. Since

the number of subjects included three males and five females the findings are limited in applicability to larger and different groups of animals. However, in terms of the present population the hypothesis was supported.

Similarly, Hypothesis V, which states that relatively stable positions will be maintained by males in the group, was supported by the data and was also accepted. The positions of males, even when the number was increased to three males, was found to remain stable whether in the dyad, the triad, or in groups as large as eight.

Hypotheses VI and VII both pertain to the formation of coalitions when the number of individuals increased within a relatively small area of space. It should be pointed out that two different kinds of coalitions were discussed by Hodan and this differentiation was kept in mind in the present study. Overt coalitions are defined as those in which two or more subjects are observed to attack a third subject, and therefore open aggression had to be present before an overt coalition was said to exist.

Another type of coalition discussed by Hodan and used for predictions in the present investigation was the "statistical coalition" in which the outcome was predicted on the basis of the relative powers possessed by the subjects in combination, regardless of actual aggression observed. While the hypotheses of the present investigation pertain only to those instances in which overt coalitions occurred, statistical coalitions were predicted and

tested out also and enter into later discussion. It is very possible in primate studies that an implicit and subtle effect may be consequent to the mere presence of certain animals so that the behavior of others in the group are affected. This possibility is suggested by observations in both the wild and in captivity that the dominance of an animal is influenced by the presence of other higher-ranking individuals with whom the animal has a special relationship. Such effects might well be conceptualized as the result of relatively stable alliances over a period of time. The proximity of animals with such alliances were not specifically predicted in the hypotheses, but are dealt with in the general terms of "statistical coalitions." The results show that out of a possible 84 trials which comprised the complete testing of all dominant-subordinate groups in the first part of the study, many fewer coalitions occurred than would be expected upon the basis of current coalition theory in humans (Caplow, 1956; 1959; Gamson, 1961). It should be noted that for such theory to apply to the present data, extention from the triadic situation to larger groups of individuals would be required. At the present time the indications are that coalition theory can be successfully extended to the tetrad (Willis, 1962). Predictions based on the original power of individuals in the dyad would lead to an expectation of coalitions on any or all of 60 of the trials. Only two overt coalitions occurred, however, and both of these were formed within the same group comprised of W and all "subordinate" chimpanzees. In both cases the coalitions were comprised of the dominant plus the lower-

ranking members against the animal second in line. Since the formation of overt coalitions was a relatively rare event, there is insufficient data to support or refute Hypothesis VI. The data is in line with the prediction, however, and seems to suggest that when overt coalitions form they are composed of top and bottom animals against the second-ranking member of the group. The data indicates that increased numbers up to eight individuals in a relatively small area does not result in more coalitions than occurred in triads. The opposite effect occurred, in fact, so that there was a reduction in number of coalitions. Hypothesis VII was therefore rejected.

Hypothesis VIII stated that individual aggression increases as the number of individuals increases within restricted space. Utilizing the behavioral taxonomies presented by Hodan (1970) and Wilson and Wilson (1968) it was possible to keep a frequency count of all agonistic behaviors observed under the two experimental conditions. Aggression was then related to the number of subjects present. It was found that there were no instances of aggression against the Alpha and Beta animals even though these groups were relatively large. Against the animal expected to be third in line, W, there was a successful statistical coalition but no individual aggression. The aggression during that group series consisted of five animals attacking the challenger together on two different occasions, thus forming two overt coalitions.

As previously planned in the event that significant dominance did not emerge, further study of the group behavior was

carried out to attempt to determine whether individual, coalition, or group size effects could be identified. The results shown in Table 2 indicate that with the third and fourth animals, just the number of subordinates alone did not determine whether the dominant animal would be overthrown. When Mi was removed from the Group W retained dominance, and when W was removed from the group Mi maintained dominance. Most of the aggression, coalition or individual, took place when these two animals were both present in the group and in competition. The coalitions were not against the dominant chimpanzee but rather appeared to function in support of the dominant animal. No particular combinations of animals were found to be effective against an animal. Table 2 suggests that dominance interactions between individuals is the significant variable in dominance position shifts rather than group size, group composition, or overt coalitions. Similarly, two instances of individual aggression were observed in the Pe-Ca-Me group although no coalition was observed. The significant factor seemed to be the competition of another individual. The best predictor of dominance "overthrows" seemed to be measures of individual distance between competing animals. Individual aggression did not increase as a function of increased numbers, and Hypothesis VIII was rejected.

The hypotheses of part three have to do with the effects of increased space on individual and group behavior in a food competition situation. The relatively clear results obtained when dyads and triads were tested in a situation of increased space points to the possibility of greater social variability and a

loosening of the dominance structure as space is enlarged. The results of the previous study (Hodan, 1970) showed, as a matter of fact, that a significant dominance hierarchy no longer existed in the two cage condition. The present study was therefore expected to confirm again the finding that chimpanzee social structure becomes more loosely organized when there is more adequate social spacing.

An examination of the emergent dominance hierarchy in the 2 cage condition (Table 5) reveals that there was only one exception to a completely transitive linear dominance hierarchy. This one exception was that in which two top ranking females tied in the number of grapes each obtained. The remainder of the chi-square values show that there were significant individual distances between all of the other chimpanzees in the linear dominance hierarchy. Therefore the dominance hierarchy was even more clearly structured in the 2 cage situation than it was in the one cage condition. (See Table 3) Hypothesis IX was subsequently rejected.

Hypothesis X stated that changes in the linear dominance hierarchy would take place between females adjacent to each other. An examination of the hierarchy which emerged when space was increased shows that shifts took place for five subjects (Figure 1). Four of these S's were females and one was male. These shifts in position consisted of two top ranking females moving more closely together so that theywere in fact not differentiated in position, the third female becoming clearly differentiated in position, and the next three S's completely reversing positions. The one male

Table 4

Chi-square Values for Triads in the Two Cage Condition (from Hodan)

Critical Values

$x^2 = 12.00, p \leq .001$; $x^2 = 8.32, p \leq .005$; $x^2 = 5.32, p \leq .025$; $x^2 = 3.00, p \leq .10$

	W/Mo	W/Mi	W/Pe	W/Ca	W/Me	Mo/Mi	Mo/Pe	Mo/Ca	Mo/Me	Mi/Pe
P	5.32	5.32	1.32+	12.00	8.32	12.00	12.00	12.00	12.00	5.32
W						12.00+	1.32+	12.00+	8.32+	.32+
Mo										1.32+
Mi										
Pe										

Note. A + sign following a chi-square value indicates an effective coalition.

Table 4 (continued)

Chi-square Values for Triads in the Two Cage Condition (from Hodan)

Critical Values

$x^2 = 12.00, p \leq .001$; $x^2 = 8.32, p \leq .005$; $x^2 = 5.32, p \leq .025$; $x^2 = 3.00, p \leq .10$

	Mi/Ca	Mi/Me	Pe/Ca	Pe/Me	Ca/Me
P	12.00	12.00	12.00	12.00	12.00
W	.32+	0.00+	5.32+	1.32+	3.00
Mo	12.00	.32+	8.32	8.32	12.00
Mi			1.32+	12.00	12.00
Pe					1.32+

Note. A + sign following a chi-square value indicates an effective coalition.

Table 5

Chi-square Values for All Groups in the Two Cage Condition

Critical Values

$x^2 = 12.00$, $p \leq .001$; $x^2 = 8.33$, $p \leq .005$; $x^2 = 5.33$, $p \leq .025$; $x^2 = 3.00$, $p \leq .10$

	Mo W Mi Ca Pe Se Me	W Mi Ca Pe Se Me	Mo Mi Ca Pe Se Me	Mi Ca Pe Se Me	Mi Ca Pe Se Me	Ca Pe Se Me	Pe Se Me	Se Me	Me
P Mo W Mi Ca Pe Se Me	3.00	0.00	0.00	12.00	8.33	3.00	5.33	12.00	12.00

Space Fixed, No. of Animals Varied (Hodan)

One Cage		Two Cages	
2 Ss	3 Ss	2 Ss	3 Ss
P	P	P	P
W	Mo	Mo	Mo
Mo	W	Ca	Mi
Mi	Mi	Mi	W
Pe	Pe	W	Ca
Ca	Ca	Pe	Pe
Me	Me	Me	Me

No. Of Animals Fixed, Space Varied (Hodan)

2 Ss		3 Ss	
One Cage	Two Cages	One Cage	Two Cages
P	P	P	P
W	Mo	Mo	Mo
Mo	Ca	W	Mi
Mi	Mi	Mi	W
Pe	W	Pe	Ca
Ca	Pe	Ca	Pe
Me	Me	Me	Me

All Dominant-subordinate Groups with Space Varied (King)

One Cage	Two Cages
P	P
Mo	Mo-W
Mi-W	Mi
Se	Ca
Pe	Pe
Ca	Se
Me	Me

Figure 1. Changes in the dominance hierarchy as a function of space and the number of animals.

S_e who underwent a position change did so passively in that he was "left behind" the others in number of grapes obtained. The data supported the hypothesis and it was accepted.

Hypothesis XI predicted greater stability for males in the hierarchy than for females under conditions of increased space. Two of the three males maintained their positions while the third dropped from fifth to seventh place. The data was not sufficient to make generalization to other populations, but in terms of the subjects of this investigation the hypothesis appears to be supported.

Coalitions in the 2 cage condition were expected to decrease in number but to have the same general structure as in the one cage situation. Rather surprising results were obtained in that the number of overt coalitions increased significantly when space was increased. This finding was in direct contrast to previous findings (Hodan, 1970; Pearce, 1970) which showed either a drastic decrease in coalitions or the same level of insignificance in the 2 cage condition. The present study showed that overt coalitions increased from two in the one cage to six in the two cage, a tripling in number. Furthermore, the coalitions took place within more groups than before: within the groups of the Alpha, Beta, and third-ranking animals. No overt coalitions occurred in any of the remaining groups. The structure of the coalitions and the apparent function was again like that found in the one cage condition in both this study and that using triads. In all cases the members of the coalition functioned in concert to attack the

"challengers" who was obtaining grapes instead of the dominant chimpanzee. Where the dominance of the animal appeared to be in some question and perhaps not yet settled among the members in that situation, the coalitions then divided or alternated in function so that they attacked first one animal and then the other of the two competing animals. From observation it seemed very much as if the group was quickly and appropriately aware of the lack of clear leadership or dominance. Thus the initial impression that the structure of chimpanzee coalitions consists of the top and bottom ranking animals against the challenger in the middle received confirmation, but the assumption that the challenger will always be the animal second in rank was refuted. Hypothesis XII was therefore accepted. Hypothesis XIII which stated that the number of coalitions should decrease with an increase in space was not supported by the data and was consequently rejected.

Hypothesis XIV asserts that the amount of individual aggression will decrease as a function of increased space. The surprising results revealed that the opposite proved to be the case: instances of individual aggression increased significantly in the 2 cage condition. Whereas only two instances of individual aggression (that occurring outside coalition behavior) were observed during the first spatial condition of the study, 23 instances of overt individual aggression occurred during the second condition in which space was increased. (Figure 2) The fact of an increase in aggression over ten times as great in the 2 cage situation led

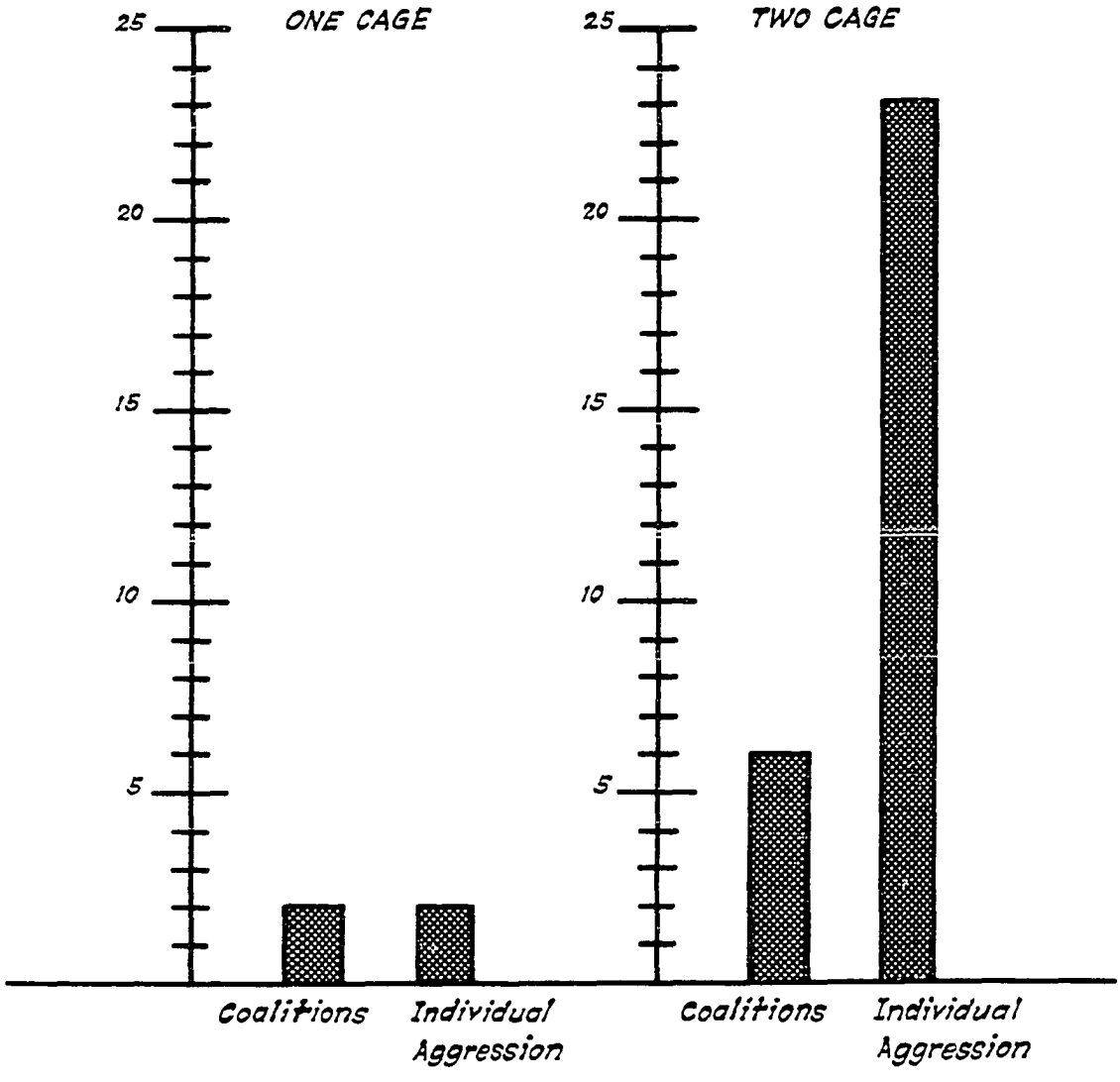


Figure 2. The number of overt coalitions and individual aggressive behaviors in the one-cage and two-cage conditions.

to an emphatic rejection of the hypothesis. A two population proportion test (Walker and Lev, 1953, pp. 77-78) resulted in a z of -4.553 ($p \leq .0001$) and it can therefore be seen that the increase in coalitions was highly significant.

It was previously pointed out that the results for the fourth male subject, Mu, would be reported and discussed separately from the rest of the data. In many ways this animal was atypical in the group by virtue of age, size, and behavior. In the one cage condition Mu sat passively not taking any overt part in the experimental task. He did not seek nor obtain any of the grapes available in any of the groups. In contrast to what might be expected in terms of dominance behavior from the oldest, largest male of the group, Mu did not assert himself during any of the trials. On the other hand, during the complete set of dyads which were run prior to the testing of the larger groups, Mu obtained grapes in six out of a total of eight dyads in which he took part. He obtained five out of a possible 12 grapes with each of the highest ranking chimpanzees: P, Mo, and W. He took all 12 grapes from each of the two other males, Se and Me. It was thus very apparent that Mu could have functioned in a much more dominant manner during the group trials, but for some unknown reason did not.

The two cage condition brought out a phenomenon which illustrates Mu's indirect influence on group behavior. Even though he did not obtain a significant number of grapes in any of the groups, his presence so affected the behavior of the other chimpanzees that the dominance hierarchy already established almost

ceased to exist. P became very "passive" in behavior for the first and only time during the entire experiment whereas normally he functions as a highly dominant male. The Beta animal Mo also became extremely passive when Mu was placed in the group with her, and she was never passive in a situation in which she was dominant or had some chance to attain dominance. The third and fourth ranking females in the hierarchy derived the most benefit from Mu's presence. They both seemed to take advantage of the sudden lack of dominance at the top so that they had opportunity to take grapes unimpeded. The amount of aggression observed fell to zero, no coalitions were formed, and what amounted to a complete loss of social structure resulted. It was clear that Mu was highly regarded by the others but that his dominance position was not definitely established since he would not "play the game" in the experiment as did the other subjects.

One interpretation of the effects of Mu's inclusion into the groups which is probable is that the chimpanzees closest to Mu in dominance were careful not to become involved in direct confrontation with him. His great size and strength in comparison to the other animals brought immediate respect whenever he was in close proximity. Additionally, Mu seemed to find the experimental procedures "against his dignity" throughout, and he pretty much went his own way as he wished.

In summary, the results of this study were in direct contrast to those expected on the basis of previous investigation. The effects of increased numbers of individuals under two spatial

conditions had been expected to produce a break-down in the social order through increased social stress, many more instances of aggressive behavior through relative crowding, an increase in coalitions due to the break-down of the dominance hierarchy, and perhaps an even more dramatic effect from increase in space than was true when just triads were used. The results revealed that under conditions of very restricted space and crowding the chimpanzees formed a more tightly organized and clearly differentiated linear dominance hierarchy which seemed to be based upon the amount of individual distance between and among the animals. Rather than having a "loosening" effect on the dominance organization as predicted, the increase of space produced a linear dominance hierarchy with a slightly larger number of significant X^2s than in the one cage condition. More aggression in the form of individual challenges occurred in the two cage condition at a highly significant level rather than under the condition of greatest crowding. Also more coalitions took place when space was increased, the number of overt coalitions tripling in the two cage condition.

CHAPTER V

DISCUSSION

The present study and two previous, closely related studies (Hodan and Pearce) have demonstrated by somewhat different means that groups of captive chimpanzees will form a linear dominance hierarchy when placed in a competitive, food-getting situation. The subjects used had lived together over a period of many months or years, and they were trained in the experimental task and then tested and observed all within part of their normal living quarters. Thus the testing conditions approximated normal living conditions as closely as possible, and the experimental procedures were designed to tap and expose already existing social relationships and social structure. The extent to which the experiment served to create new relationships and social structure rather than reveal more clearly the underlying order is open to question and further investigation. Certainly food competition is not a new experience for this group of chimpanzees, and certainly life in the colony proceded prior to, during, and following the studies. The present writer tends to believe that the behavior elicited by the experimental situation heightened and brought more clearly into view the social structure which can be observed in other contexts in the daily life of the colony. It is very possible,

on the other hand, that the competition set up experimentally tended to solidify the dominance hierarchy to some extent not present in normal daily encounters prior to the experiment. The chimpanzees rather quickly learned to operate the apparatus and generally appeared eager to enter into "playing the experimental game." Successes and failures in obtaining grapes were readily observable by all the chimpanzees, and the public exposure of outcomes of dominance interactions may have lead to more clearly differentiated status positions outside the test situation. However, the test conditions did not create chimpanzee behaviors which did not already exist actually or potentially, and the results bear out the predictions that under certain conditions chimpanzees will become socially organized in a way which can be described by means of a linear dominance hierarchy. That the experimental conditions do not represent exactly living conditions in the wild is not only true but is the point of the investigation. Primates, human and otherwise, can be expected to adapt themselves in certain ways to certain conditions of living, and that adaptions to restricted space and crowding will differ from behavior adaptations to the natural habitat. The ways in which chimpanzees become organized, the ways in which social behavior functions and changes, and behavioral analogies with humans under somewhat comparable circumstances are of major interest to the present investigator.

The results showed that contrary to prediction the linear dominance hierarchy remained clearly defined, even moreso, when space was increased. This finding relates to the increased number

of subjects present as well as to increased physical space. The effects of increased numbers and increased physical space were not directly opposite as shown by the very different results in the one cage and the two cage conditions. Had reduced space and crowding been the same in effect, the results from the two conditions would have been the same or more nearly similar. With relatively small numbers of subjects held constant (dyads and triads only), increased space produced so many changes in rank order and in distances between individual chimpanzees that a significant linear dominance hierarchy was no longer considered to exist, (Hodan, 1970). With increased numbers of individuals in groups comprised of each chimpanzee and all those below him or her in rank, greater space and larger numbers of individual do not just cancel each other out. Rather, the results show that increased space leads to an even more clearly structured social organization but also tends to bring about a significant increase in interpersonal conflicts. The presence of more individuals in both spatial conditions probably led to the formation of a clearly differentiated social structure for both. However the presence of more individuals in the one cage condition also resulted in a significant decrease in coalitions and in the amount of aggressive behaviors of all sorts. Whereas one might expect a collapse of social structure in the one cage conditions as a direct consequence of crowding and openly expressed aggression, the opposite was the case. Social structure remained tight and aggression was reduced to almost zero. Whereas it was expected that the social structure

would collapse in the two cage condition as a direct consequence of all the chimpanzees having a more nearly equal chance at obtaining grapes because of greater physical distances from each other, more avenues of escape, etc., again the opposite was the case. Social structure consisted of an even more significant dominance hierarchy overall, albeit a less rigidly organized one. Whereas less aggression and fewer overt coalitions were predicted under the condition of increased space because of less social contact and social stress, again the opposite proved true. Significant increases in both overt coalitions and individual aggressive behaviors occurred in the two cage condition.

Greater social flexibility in the two cage condition is reflected in smaller chi-square values, although still significant, for several animals at the top of the hierarchy and an advance in position for others at the bottom. The finding that several lower-ranking subjects reversed their status positions in the two cage condition is similar to the reversal which occurred in a previous study with a different group (Pearce, 1970). Clearly some individuals did better when space was increased and their individual behavioral characteristics had freer range. An animal who might not risk the direct confrontation which would occur in the one cage condition might take advantage of circumstances which place a greater strain on a more dominant animal's ability to maintain dominance. Females were especially prone to become manipulative and even devious in obtaining grapes when they were not clearly dominant, and the two cage situation offered more opportunity for such behaviors.

Females also proved to be the most highly competitive and openly aggressive, unlike earlier observations (Hodan, 1970). The males in the group, with the exception of the top ranking male, P, were all relatively passive individuals compared to the females. Se was an unusually passive male whose behavior is probably the result of his having been reared by humans in a totally human environment thus becoming human oriented rather than chimpanzee oriented. He often did not seem to have appropriate chimpanzee behavior; for example, he did not appear capable of distinguishing playful from nonplayful aggression. Se frequently displayed signs of fearfulness regarding his genitalia when around his more agressive associates and was often observed clutching himself when in the company of either P or Mu. Most of the time Mu remained aloof and passive with the other chimpanzees. He often behaved as if to convey an impression that he "did not see" what was going on at all. This male was also reared in a human environment although later had many years of experience in a zoo with three female chimpanzees. Me, the lowest ranking animal, never was able to assert himself effectively enough to obtain the grapes he obviously wished to have nor did he ever advance in rank. He was often involved in aggressive encounters but always in concert with others and never all by himself. He seemed to take advantage of every opportunity to engage in agressive behavior toward other animals, but frequently he turned the aggression onto himself through pulling his own hair or stiking at his own head.

By far the greater number of open challenges to dominance

arose among the three top ranking females: W, Mo, and Mi. There was a certain amount of instability in the behavior of all three animals, some of which may have been related to fairly subtle changes in the estrus cycle or to other hormonal activity. This instability seemed to bring the females into closer approximation in dominance at some times. W was the most unstable female of all, and she was observed to undergo frequent changes in her relationships to both chimpanzees and humans in and out of the experimental situation.

The finding that the two cage condition did not reduce individual distances to the extent expected may have been partly a function of the larger groups of individuals present, sometimes as many as eight. Since both spatial conditions involved relative crowding, the increase in space in the two cage condition may not have been sufficient to permit the looseness and openness of structure revealed with dyads and triads. Perhaps a condition of greatly increased space would yield results more like those previously reported. What was observed to occur when the groups were placed in the two cage situation was an even more significant linear dominance hierarchy, but much more flexibility in structure was present. The dominant animals held their positions, except for equal dominance for the second and third ranking females, but dominance was not held with such absolute rigidity. In other words, more chimpanzees were able to obtain grapes in the two cage situation but the social order did not collapse.

The question arises why increased space produced much

more aggression in the form of coalitions and individual attacks. One possible explanation is that through greater flexibility in social organization and more individual freedom of expression, overt aggression could be expressed and "tolerated." Aggression in the two cage condition may not have posed the threat that it did in the one cage where there was very little space to move around in and practically no chance to escape attack. The results indicate that there can be too little space and too much crowding for overt aggression to occur. Chimpanzees seem to maintain individual distances under conditions of crowding just as other species do, and the function may well be that of reducing aggression significantly. The results point to the possibility of a critical individual distance which determines the triggering of aggressive interaction. The critical level of individual spacing may have been surpassed in the two cage situation so that aggression was somehow at a safer level in the groups and could be released. A critical level of individual distances relating to the release of aggression may arise out of what might be thought of as a critical ratio between space and crowding. The present study with previous similar studies seem to indicate that aggression all but disappears under restricted space and relative crowding, that it reappears as space is increased, and that once again it all but disappears when the amount of space per animal reaches a certain level. What that level might be is left for further investigation of these and other variables which may be involved.

The data of the present study lends support to the concept of individual distance requirements at the nonhuman primate level. Humans have been observed to react negatively to an invasion of personal space, and similarly chimpanzees may mediate important behaviors such as aggression by means of individual space. The notion that crowding and overt aggression are positively correlated is not exactly true according to the present findings. Instead there appears to be a critical point in spatial relations at which aggression may be released or more easily released. There are indications that there may be another critical point at which space is sufficient to all but eliminate overt aggression in the normal course of things. Chimpanzees in the wild reportedly live their lives in relative tranquility and with great openness in social relations, and aggressive encounters when they do happen may well be related to a breakdown of spatial boundaries.

Another finding regarding features of individual space was that there is not necessarily "more room at the top" of the dominance hierarchy. All of the chimpanzees throughout the hierarchy were sometimes more dominant than at other times regardless of their relative position in status. Individuals at the top did not always enjoy full sway and individuals toward the bottom in one situation might change positions in another situation. Dominance positions seemed to be changing and flexible depending upon individual personality characteristics and interpersonal relationships. The solidity of social structure revealed in both the one cage and two cage conditions may tend to cover up the great intra-

group flexibility actually observed over a long period of time. Chimpanzees are highly adaptive primates with a wide behavioral repertory and great subtlety in social communication. The major finding of this study may well be the direct observation that roles were reversed, individual distances were reduced, interpersonal competition was at a very high level, individual idiosyncracies were brought into play, and yet the social organization of the group remained intact and did not collapse. It is tempting to conclude that chimpanzees seem to have a talent for democratic process.

With regard to the formation of coalitions, the data of this study shows especially clearly a particular type of structure in chimpanzee coalitions, and a particular function as well. The larger groups of individuals permitted a relatively sharp view of the way coalitions come about and the ends they appear to serve within the total group. The findings are generally in accord with those previously reported for triads (Hodan, 1970). Without attempting to generalize to other chimpanzee populations, the data showed that coalitions served to support the existing lines of dominance or power in the group and in this way worked against social change. Each and every time a coalition formed and functioned, the situation was one in which a chimpanzee other than the dominant animal took a grape and perhaps even contined to challenge the dominant animal. The challenger did not have to be the second ranking individual as previously assumed but usually challenges came from the second ranking chimpanzee. Coalitions were formed instantaneously,

as if triggered automatically, and always consisted of the top ranking plus all the rest of the group who together would attack the "rebellious" animal. An interesting phenomenon was observed to occur where dominance was nearly equal between two chimpanzees and therefore not yet settled. The coalition shifted the focus of attack from one to the other as if to reinforce the attempts of the "leaders" to gain power, and in reflection of the ambivalent state of things. One is reminded of the "flocking" behavior of birds in which the entire group attacks an intruder. In terms of sociological terminology, chimpanzee coalitions can be described as "functional" and supportive of social stability rather than "dysfunctional" and supportive of social change and instability.

Coalitions consisting of animals who had fairly well established relationships were not observed. A special relationship of some sort between a dominant and subdominant animal seemed to encourage the less dominant individual to take grapes with relatively little fear of retaliation. Thus in the two cage condition W took grapes away from P at certain times with apparent freedom. Coalitions, however, transcended special friendships and alliances and seemed to be a built-in feature of social organization.

The question arises why so few coalitions occurred throughout the study. Coalition theory based on sociological study (Caplow, 1956; 1959; Gamson, 1961) of coalitions in humans would lead to a prediction of many more coalitions than actually

occurred. The theory that individuals will form coalitions in order to maximize their gains seems not to apply to chimpanzees. Neither this nor the previous study with the same population of chimpanzees showed that coalitions resulted in the members of the coalition receiving more food reward. Instead, the top ranking and subordinate chimpanzees united against a chimpanzee who seemed to be taking a grape "inappropriately." At the end of the trials members of the coalition did not increase their "take" through joining. Chimpanzee coalitions are as yet incompletely described and understood, however, since animals were sometimes observed to take grapes away from the dominant individual without setting off a coalition against him. Why coalitions happened at certain times and not others can not be explained on the basis of the present data. One tentative interpretation is that two group characteristics may be relevant to the formation of coalitions. One factor may be whether or not aggression of any sort can be "allowed" in the situation as previously discussed with regard to individual attacks. A second factor may pertain to the strength of the social structure in the group. Other investigators of primate groups have reported that the strength of the leader, and the presence of the leader in the group, determines in large part the amount of group aggression and group cohesiveness. It is suggested by the present writer that the stability of the social group may be directly responsible for the number of coalitions which will occur. Since the present population of colony chimpanzees is relatively stable because living conditions tend to remain stable over long periods

of time, the relative social stability of this group may mitigate against coalition formation. Social stability proved to remain characteristic of this population even under intense competition for power and food in circumstances of very little physical space and what amounted to overcrowding for this group. Under such conditions there would be little occasion for coalitions to form in defense of the status quo in power relations. Perhaps chimpanzee social structure in the wild is actually very strong and durable so that challenges and changes rarely occur and rarely are observed. Flexibility in social organization is quite different from weakness of social structure, and in fact may be just the opposite. In the microcosm of the laboratory situation, chimpanzees quickly and effectively form a definite and very servicable social organization.

Differences in group behavior as a function of the particular "leader" present were evident. For example, P's group appeared to respect his authority and to be accepting of his role as the dominant individual. W's group, on the other hand, took advantage of her uncertainty about her own dominance. Throughout the study W's presence in a group almost always went along with group change, aggression, and heightened group tension. Similarly Mu's presence in a group, at least in the two cage condition, resulted in great group instability and a general uncertainty. Mu's presence therefore had a disruptive effect which may have been the product of his potential but as yet unestablished dominance within the group.

Two features of coalition formation are suggested for further investigation. One is the apparent relationship between

group stability and coalitions. Different types of leaders and different stages of group instability might throw further light on this phenomenon. A different experimental task in which dominance would be open to question might reveal more information about the correlation between group instability and coalitions. Thus the weakness of the leader may turn out to be the relevant variable rather than the weakness of subordinates as in human coalition theory. The second feature for future study is the relationship between individual spacing, perhaps a critical ratio between individual distance and physical space requirements, and coalition formation. Physical space can apparently be too small for coalitions to emerge in any significant way. On the other hand Hodan's results showed that physical space can be large enough so that coalitions do not occur to any significant extent. An interaction effect between numbers of individuals and amount of physical space is indicated as being relevant to the release of coalition behavior.

Social Behavior and Individual Differences

Several features of individual development seemed important to effective social interaction within this captive population. There were wide differences in ability to perceive correctly the meaning and intentions communicated in the behavior of others. There were wide variations in the quality of aggression expressed by different animals, from milder forms as in simple self-assertion to open attacks in which wounds were opened up and bleeding occurred. The Alpha male, P, was usually able to maintain

dominance in the test situation merely by his presence or a gesture or look. Similar observations were made in the daily colony life in which P was always first and always the one deferred to, with the exception of Mu whose position was somewhat undetermined. Periodically P was observed to engage in very loud, aggressive displays during which he banged one foot on a metal door producing a sound which reverberated throughout the lab and following which he leaped forward toward one of the other chimpanzees, striking at them or even pounding them as he went by. Generally he seemed very friendly and amiable toward the others.

Me was always "low man" in every encounter and he was in an almost constant state of frustration and consequently he frequently was seen striking at someone, throwing "tantrums," pulling at his own hair or hitting his own head, or screaming. Me always seemed to be very quick to react aggressively but never effective in getting what he wanted.

Se might aptly be described as "Mr. Nice" since he was usually obsequious and deferential to all higher ranking individuals: putting his arm around them, seeking them out to groom them whether they had indicated they wanted to be groomed or not, and often placing himself protectively behind either Mu or P. There was thus a passive-aggressive quality about Se's behavior. He was much more atuned to humans than to chimpanzees, apparently, and he was quick to seek approval from humans in a way which was un-chimpanzee-like. Se avoided all open encounters with the other animals and often displayed concern for the safety of his genital

region. During fights he was usually observed up on a shelf away from the participants or even in another room.

Mo was an unusual female in terms of her rather simple, straight-forward communications. Unlike some of the other females, Mo never engaged in a "sneak attack" on humans and her aggression was clearly communicated toward chimpanzees and humans alike around the laboratory. In other words, Mo was much more like males in that she was relatively easy to predict in her behavior. She tended to be highly dominant in the group, and even P treated her with obvious respect. At times, depending upon the relationships with P, the two females Mo and W appeared to change somewhat in their relative status. Mo's background included much experience with both humans and chimpanzees as part of a troop of "show business" animals. Mo was clever in being able to learn quickly and perform tricks. Her ability to grasp and respond to human statements was sometimes startling. Mo seemed to be accurate in her perceptions of relative dominance, and her behavior was usually appropriate to what she could accomplish. If she was with a more dominant animal, such as P or Mu, she would withdraw from the situation or become very passive. If there was a good chance for her to come out on top she did so.

The four middle females were highly aggressive animals who were almost always making the most of every opportunity to obtain grapes. W was by far the most unpredictable animal of all in the group, and her tendency to vascilate in dominance and to show wide variations in her relationships with both humans and

chimpanzees has been true since she first entered the colony in 1965. We seemed to expect frustration and to be very intolerant of not having her way, and her attacks on humans and chimpanzees alike would come suddenly and without much warning. Mi was a very competitive female who seemed to be very intelligent and appropriate in her behavior. She was quick to assert herself and attempt to gain dominance, and she did not back down easily. She tended to be friendly toward humans and has had more human contact than most of the others since joining the colony. Pe and Ca both were highly aggressive and opportunistic in finding ways to get grapes. What they could not accomplish through direct force they attempted to do through indirection and delay tactics. Many sessions were held up for a half hour to an hour while one or both of these females held onto a nickel and refused to put it into the coin slot until the other animals seemed to have lost interest in the procedures. Both of them engaged in much "play" while holding onto nickels as if to try to outwit the others. At one point Ca managed to collect a whole mouthful of nickels which she seemed to be saving up. Pe watched the others very carefully, and the moment that she noticed a more dominant chimpanzee losing interest or apparently becoming distracted, Pe would quickly drop a nickel in and race to the grape dispenser.

Observations of these animals showed that the individual styles of aggressiveness were widely varying and subject to the effects of earlier learning. Unlike previous finding with primates isolated from the species (Mason)(rhesus monkeys), the present

data revealed that social isolation does not necessarily determine greater aggressiveness. Isolation from the species does affect communication behavior, ability to respond appropriately to behavioral cues, and skill at predicting the behavior of other individuals.

Finally, the study demonstrated that chimpanzees in captivity can acquire and maintain a wide range of behavior and great behavioral flexibility. The subjects in this investigation were all alert, active, developing individuals. Much can be learned about chimpanzee behavior and capacities from such animals. Their individuality was clearly evident and presents opportunity for future study. The experimental task provided a complex social situation in which the subjects were free to behave in a variety of ways, and they did. Dominance behavior was not forced upon them through artificial means but developed out of complex social interactions.

CHAPTER VI

SUMMARY

This investigation was designed to determine whether and when a group of captive chimpanzees become socially organized into a straightline dominance hierarchy or other form of hierarchy. The method of testing was a direct test of each chimpanzee in competition with all others in the group below him in dominance. This method is a departure from previous dominance studies in which the presence of a dominance hierarchy has been presumed to exist upon the basis of all possible dyads or triads, and subsequent ranking. The very different results obtained in previous related studies in which space was increased from a one cage to a two cage situation (Hodan, 1970; Pearce, 1970) led to further study of the spatial factor. The major interest was in the type of social organization which both females and males of different ages might develop under circumstances of intense competition when space was relatively small and behavior confined or when space was larger and behavior possibly more open. The factor of increased numbers of individuals above dyads and triads up to and including eight subjects was a significant variable throughout both spatial conditions so that number of individuals (relative crowding) and physical space could be observed separately in their effects upon dominance behavior.

Observations on chimpanzees in the wild indicate that no discernible social organization exists, but that rather there are situational expressions of dominance which vary and in which patterns have not been clearly defined and described. In general, males in the wild tend to be dominant over females although reports are not consistent in this respect, and the variables as yet remain undetermined with the exception of the effects of estrus on female dominance. It has been reported that females in their natural habitat do not form a dominance hierarchy, and that adults are dominant over infants.

The close relationship between chimpanzees and humans makes the study of chimpanzee social behavior relevant to problems of human society as well as being interesting in and of itself. Problems of human crowding, social stress, and aggression are of particular importance in modern day life. The literature indicates that both humans and many animals behave very differently when they are confined to small spaces and when they are subjected to crowded conditions. At the present time all species including man appear to be endangered both in terms of survival and in terms of the quality of life which an increasingly complex civilization jeopardizes. Relevance to human social problems makes the study of life in the wild a basis for comparison, but hardly comparable to conditions under which the vast majority of human beings live. The study of captive chimpanzee groups is one opportunity to view and study social behavior and social organization under circumstances of reduced space and increased interpersonal contact.

The nine chimpanzees used in the study all appear to be healthy, well developing individuals. They did indeed become organized into a linear dominance hierarchy which was directly observed when all the animals were placed together in groups of all sizes. The differences between the dominance hierarchy derived from dyads and triads proved to be essentially the same as that demonstrated when each size group was placed together: all eight, then seven, then six, etc. down to the last two. Consequently the existence of a linear dominance hierarchy under the experimental conditions in this and in the two previous, related studies can be assumed to be actual and not an artifact. The stability of the dominance relations as well as their variance were studied in relation to selected space and group-size variables so that a fairly clear picture emerges. The effects of space in relation to numbers of individuals present could be more clearly seen as groups were made larger or smaller. Differences between male and female behavior were more readily apparent in this study since more individuals were used. The popular view that males tend to be more aggressive than females, and that females tend to be more manipulative proved not to be true under the test conditions. Females were more manipulative only when size and strength and dominance failed them. In other circumstances they proved to be the most aggressive of all.

It was predicted that with the larger groups of individuals there would be a significant increase in the number of coalitions and individual expressions of aggression due to the expected social

instability. Neither social instability nor more coalitions were forthcoming in the one cage situation as anticipated, and what happened instead was an increase in coalitions and in individual attacks when space was increased. This finding was counter to the findings with dyads and triads in which increased space led to a significant decrease in coalitions, and overt aggression. Thus the numbers of individuals placed together were found to interact with the amount of space available to produce the results which make a simple interpretation of space impossible.

Two kinds of space were described and found to be important: spacing between individuals within the dominance hierarchy as statistically described, and physical space. Individual space as an interpersonal distance variable has been described for humans as "personal space." Spatial requirements for nonhuman species have not been talked about in these terms in prior investigations but rather are usually discussed in terms of physical spacing: territories, ranges, sites, etc. Dominance orders have been described for most species but not in spatial terminology in studies of animal behavior. The results showed that a concept of individual "social space" as a measure of individual distances within a dominance hierarchy did have relevance to social behavior. The triggering of overt aggression and the stability of social organization were found to be directly related to such individual distances, moreso than absolute numbers of individuals present. In fact, the best single predictor of hierarchical shifts proved to be the distance between adjacent individuals within the hierarchy. Whereas more

shifts occurred among females than among males, individual distances between females tended to be smaller and more variable and so may obscure simple female-male differences somewhat. Two spatial predictors are suggested for further investigation: (1) A ratio between physical space and numbers of individuals could probably be described in which a critical point exists at which social change will take place. Another critical point at which social change ceases may also be found, so that a "critical region" for social change could be determined. (2) Individual space as measured by distances between adjacent individuals within a dominance hierarchy may turn out to be the best single predictor of dominance challenges and social change.

The data point to the importance of individual leadership characteristics in maintaining group stability. Coalitions seemed to form in groups in which dominance was not clearly established.

A new interpretation of chimpanzee coalitions arose out of the data of the present investigation. It is hypothesized that coalitions form to perserve the social organization when group stability is threatened. The entire group was observed to attack the animal who was "out of line" in trying to take grapes. Coalitions might well be described as being functional rather than dysfunctional.

Individual differences in the expression of aggression were noted and tentatively related to early experiences with the species. Unlike the results of an investigation with rhesus monkeys, individuals isolated from the species may not necessarily react

more aggressively than others but may be more inclined to misinterpret the behavior of other animals.

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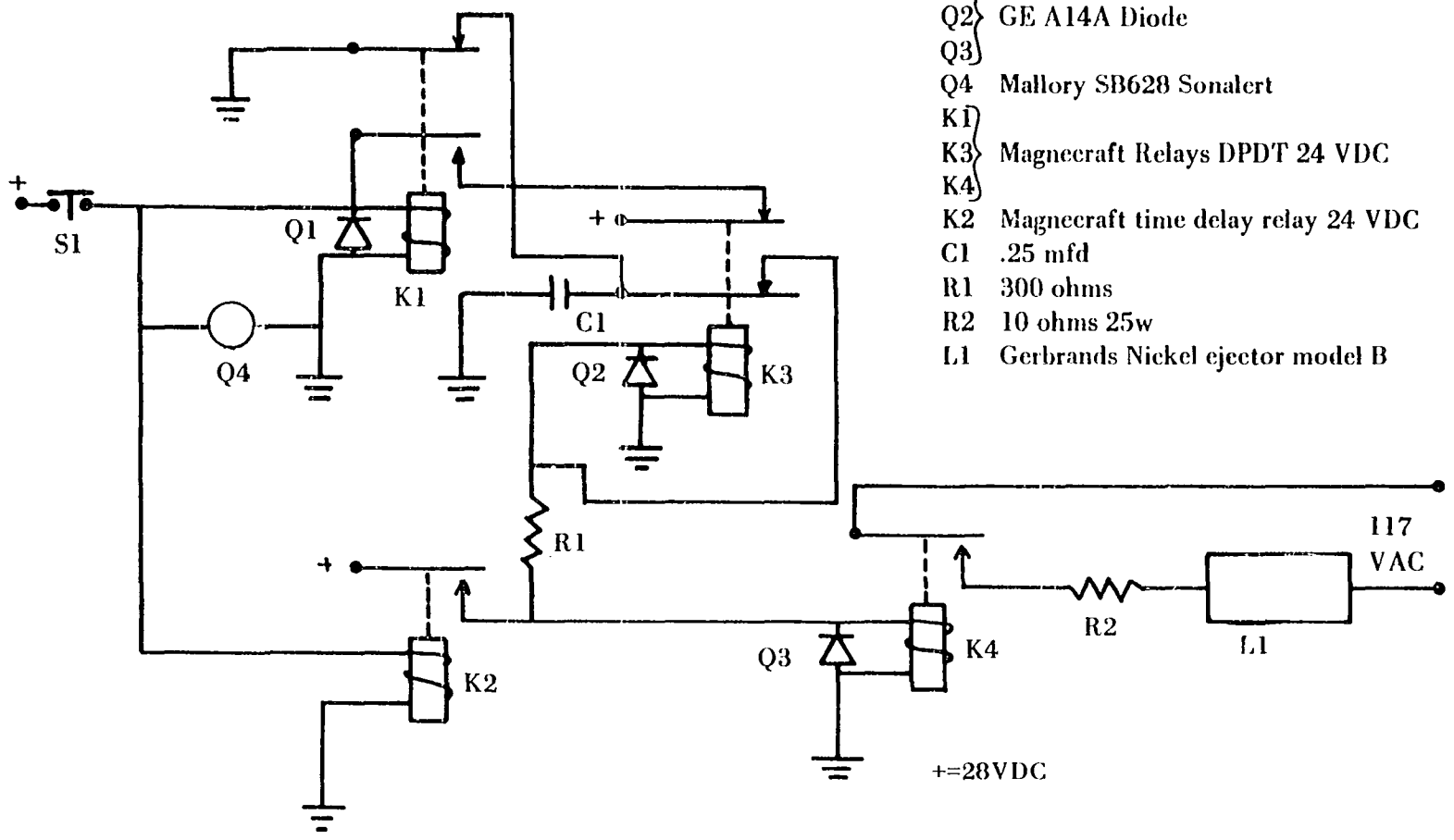
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APPENDICES

Appendix I

Delay - Alert - Coin Eject Circuit

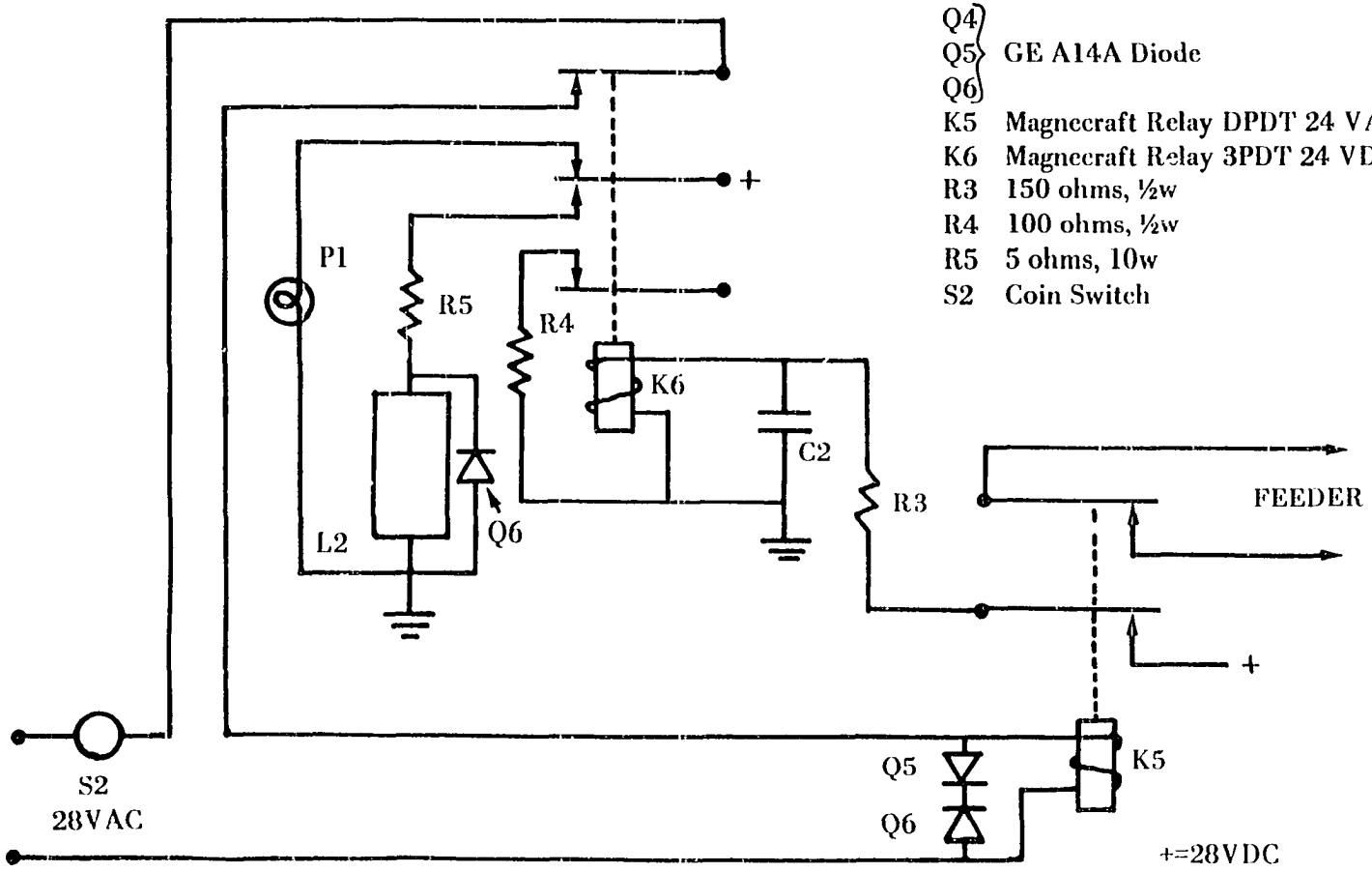


S1	Non-locking push button
Q1, Q2, Q3	GE A14A Diode
Q4	Mallory SB628 Sonalert
K1, K3, K4	Magnecraft Relays DPDT 24 VDC
K2	Magnecraft time delay relay 24 VDC
C1	.25 mfd
R1	300 ohms
R2	10 ohms 25w
L1	Gerbrands Nickel ejector model B

Appendix II

Feed - Coin Release Circuit

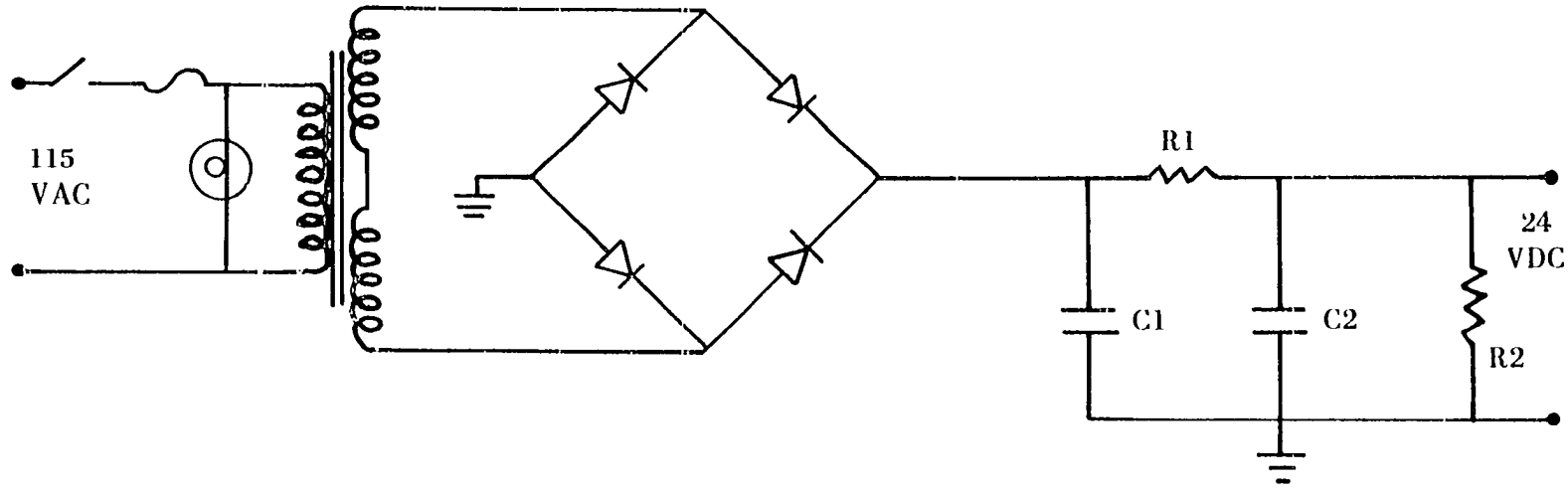
C2 5000 mfd
L2 Guardian Solenoid No. 26 24 VDC
P1 28 VDC indicator light
Q4, Q5, Q6 GE A14A Diode
K5 Magnecraft Relay DPDT 24 VAC
K6 Magnecraft Relay 3PDT 24 VDC
R3 150 ohms, ½w
R4 100 ohms, ½w
R5 5 ohms, 10w
S2 Coin Switch



Appendix III

28 Volt Direct Current Power Supply

R_1 2 ohms 50 watts
R_2 50 ohms 5 watts
C_1 1500 mfd
C_2 1500 mfd



Appendix IV

Sex and Estimated Age of Chimpanzees

Name	Sex	Estimated Age
Mutzi (Mu)	M	19
Sebastian (Se)	M	12
Mona (Mo)	F	9
Pandes (P)	M	8
Wendy (W)	F	8
Melvin (Me)	M	7
Peggy (Pe)	F	6
Mimi (Mi)	F	5
Carrie (Ca	F	5

Appendix V

Distribution of Grapes in the One Cage Condition

	P	Mo	W	Mi	Se	Pe	Ca	Me
P	12	0	0	0	0	0	0	0
Mo		12	0	0	0	0	0	0
W			6	6	0	0	0	0
Mi				12	0	0	0	0
Se					11	1	0	0
Pe						8	4	0
Ca							12	0
Me								

Appendix VI

Distribution of Grapes in the Two Cage Condition

	P	Mo	W	Mi	Ca	Pe	Se	Me
P	9	0	0	3	0	0	0	0
Mo		5	5	1	0	1	0	0
W			11	1	0	0	0	0
Mi				9	3	0	0	0
Ca					10	2	0	0
Pe						12	0	0
Se							12	0
Me								

Appendix VII

Taxonomy of Individual Aggressive Behaviors*

Attack

bite

slap

pull hair

scratch

pinch

beat on back while holding another on the floor (or kick)

throw objects at (usually tires)

lift and slam on the floor

dragged across floor

pinch or slap as run past

chase

lunge

kick as run past

Withdraw

run away

move away

turn back

ignore (look away or down)

busy oneself with other activities

Endure-Appeasement

flee

cringe or cower

present

pronated wrist

allow another to take food from hand or mouth

being groomed (tensely)

groom another (requested)

give food to another (requested)

begging gesture

passive observation (of activity of others)

Appendix VII (continued)

Endure-Appeasement

look at (head lowered)

kiss (lips or another part of the body)

smile in response to a look

"freeze" (response to a look)

touch knuckles together (or another part of body)

approach aggressor and embrace

* After Hodan

Taxonomy of Individual Agonostic Behaviors*

A. Threat

1. Intense Threat
2. Moderate Threat
3. Weak Threat
4. Weakest Threat

B. Submissive Threat

C. Threat Display

D. Chase

E. Attack

F. Submission

G. Appeasement Gestures

* After Wilson and Wilson

Appendix VIII

Experimental Cages

