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Meriones unguiculatus IN RELATION TO PHYSIOLOGY
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AGGRESSIVE BEHAVIOR OF THE MONGOLIAN GERBIL
Meriones unguiculatus IN RELATION TO
PHYSIOLOGY AND POPULATION DYNAMICS

by

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

Aggression, a topic of current interest and importance, is a catch-all term which includes a variety of responses to a variety of stimulus situations. These are grouped together largely because of their similar end results. Several authors have distinguished different types of aggressive behavior. For example, aggression is called "spontaneous" if the only identifiable stimulus is the proximity of another animal, and "competitive" if it is associated with a goal presumed to be attractive to more than one animal at the same time (Fredericson, 1950; Bevan, *et. al.*, 1960). Others have distinguished overt fighting from ritualized fighting in which no actual injury occurs (Eibl-Eibesfeldt, 1961; Lorenz, 1964; Matthews, 1964).

Aggressive behavior may also be categorized according to the objects toward which it is directed. Feshback (1964) recognizes instrumental aggression which is directed toward achievement of nonaggressive goals, and hostile aggression for which the goal is injury to some object. Examples of instrumental aggression include such things as classical conditioning in which rats fight in response to a tone stimulus (Vernon and Ulrich, 1966), operant conditioning of fighting using water as a reinforcer (Ulrich, *et. al.*, 1963), and fighting resulting from brain stimulation (Delgado, 1963, 1966).

Moyer (1967) identifies seven classes of aggression on the basis of response topography and the stimulus characteristics which will evoke them. These are, (1) predatory, (2) inter-male spontaneous, (3) terror-induced, (4) irritable, (5) territorial, (6) defense of young, and (7) instrumental aggression.

As extensive as this classification may seem, it does not include other types of aggressive behavior such as nonpredatory interspecific aggression (King, 1957a; Banks and Fox, 1968; Novak and Gets, 1969), and intraspecific female fighting. Moreover, female fighting behavior is a topic which is largely overlooked in the literature on aggression. A few studies have indicated that in several species such as the golden hamster (Kislak and Beach, 1955; Graber, 1948) and the phalorope (Hohn, 1969), the female is more aggressive than the male. Seward (1945) reported that female rats fight almost as frequently as males. Southern (1948) studied wild rabbits and found does to be particularly aggressive toward younger rabbits at the end of the breeding season. Female iguanas regularly engage in fights over egg-laying sites (Eibl-Eibesfeldt, 1961). Mature voles of either sex fight strangers with ferocity (Clarke, 1952). Allin and Banks (1968; Banks, 1968) have described the relatively high level of aggressiveness displayed by females toward male collared lemmings.

Whether females are to be considered aggressive or not also depends on the type of aggression to which one is referring. While female mice (Mus musculus) are generally nonaggressive (Lagerspetz, 1961; Anderson and Hill, 1965), they will fight competitively over food (Fredericson, 1952).

Further clarifications are necessary in order to define aggression. Kuo (1960) points out that the terms "fighting" and "aggression" should not be used interchangeably. An aggressive act of an animal may or may not involve a physical attack on another animal. "Fighting" is used only when both animals attack each other; "attacking" is used if fighting is unidirectional. Scott and Fredericson (1951) and Scott (1966) prefer the term "agonistic behavior" which includes all behavior patterns which have the common function of adaptation to situations involving physical conflict between members of the same species. In addition to overt fighting, these include escape, defensive, and passive behavior, all of which may provide adjustment to conflict.

Severity of Fighting

The question has been raised as to whether severe fighting actually exists in nature, or if it is an artifact produced by the experimental situations used to study it. In discussing overt fighting in mammals, Matthews (1964) states that "the more I have sought examples of such intraspecific overt fighting in mammals the less I have succeeded, and I doubt that it normally occurs in nature." He nevertheless goes on to list examples of fatalities which have been documented, such as in the hippopotamus and Australian bandicoots. He explains that these deaths only occur in instances of high population density. Other cases of mortality in nature directly attributable to intraspecific conflict have been reported in Indian elephants (Lorenz, 1964), field voles (Elton, 1942), terns (Palmer, 1940), red deer (Darling, 1937), muskrats (Errington, 1939), geckos and alligators (Collias, 1944), and coral fish (Lorenz, 1966).

While severe fighting has been shown to exist under natural conditions, it is probably true that fighting behavior is grossly exaggerated as a result of experimental confinement. Animals in their species-typical environment have evolved ritualized methods of avoiding destructive fighting which might be detrimental to the species (Eibl-Eibesfeldt, 1961; Lorenz, 1964). Threat behavior and stable dominance relations within social groups are other means by which destructive fighting can be prevented. However, fighting remains as a last resort when the environmental conditions are such that other behavior patterns break down.

Functions of Aggressive Behavior

The widespread occurrence of aggressive behavior in one form or another leads to the question of its possible adaptive significance. Collias (1944) noted that aggressiveness may lead to high social rank within a group, and high rank may give precedence to food, mates, and territory. Others have confirmed this relationship. Hens having high rank in the peck order have first chance at the food trough, dusting areas, the roost, and the nest boxes (Guhl, 1956). In studies on rats, those of lowest rank consistently lost weight and eventually died (Barnett, 1958a, 1963). That animals of higher rank or those which are superior fighters generally mate more frequently has been noted in lizards, *Anolis carolinesis* (Noble and Greenberg, 1941), mice (Crowcroft, 1955; Levine, *et. al.*, 1965a), wild rabbits (Southern, 1948), elephant seals (*Mirounga angustirostris*) (Le Boeuf and Peterson, 1969), red deer (Darling, 1937), and rhesus monkeys (Carpenter, 1942). High ranking female house mice in a colony moved about freely and were responsible for almost all litters produced in three experimental populations (Lloyd and Christian, 1969). In the European three-spined stickleback, the most sexually advanced female dominates and drives others from her nest site (Noble, 1938).

From the preceding examples, it seems clear that "fighting is adaptive only for the victor" (Scott, 1958). However, fighting may also be indirectly advantageous to the survival of the group or population in which it occurs. The interrelated areas in which it may have survival value are: (1) in maintaining the social organization of a group; (2) in setting up and maintaining individual or group territories; and, (3) in limiting and regulating the size of the population.

1. Social Organization

In many animals fighting is the means by which dominance or social order is determined. Once social rank is established, fighting decreases in frequency and social stability is maintained by the passive behavior of subordinates and reinforced by the threats of dominant animals.

Schjelderup-Ebbe was reportedly the first to note that chickens form a linear dominance hierarchy or "peck order" (Scott, 1958). Once the peck order has been established, pecking declines in frequency, and flock becomes peaceful and conserves energy (Guhl, 1956). Male elephant seals (Mirounga angustirostris) participate in a social hierarchy resembling that of chickens. Individual seals achieve status by fighting and maintain it by threats (Le Boeuf and Peterson, 1969). Dominance is also achieved by clashes in baboons. Afterwards there is usually a stable hierarchy in which clashes are rare (Washburn and De Vore, 1961). This also holds for other ape and monkey societies where, after dominance relationships among adult males are established, subordinates keep away from superiors (Hall, 1964).

A number of workers have observed that aggressive interactions determine and maintain the social hierarchy in house mice (Brown, 1953; Southwick, 1955a; Christian, 1963), and deermice (Sadlier, 1970). The most common type consists of one dominant male with no fighting or resistance by subordinates (Uhrich, 1938; Southwick, 1955a), but a linear hierarchy is sometimes formed (Uhrich, 1938). The value of a stable social order can be inferred from the differences between naturally growing and artificially assembled populations of mice. In growing populations fighting first occurs when the earliest litter reaches sexual maturity, and once dominance relationships are formed, fighting is sporadic and of low intensity. In assembled populations, on the other hand, fighting is immediate, intense, and prolonged (Brown, 1953).

Shortly after male rats reach maturity they enter into a round robin of fights which eventually fixes their position in the social hierarchy (Calhoun, 1962a). Calhoun (1952) has shown how the social organization in rat colonies leads to enhanced reproduction and decreased mortality when there is social stability. Barnett (1958a, 1963, 1967a) has described three types of males in a rat colony whose relationship is determined as a result of fighting. The alphas are the dominant males which are always the ones to initiate a fight. The omegas are individuals which lose weight and die after defeat by the alphas. The betas seem to be able to survive by adapting themselves to an inferior role after defeat.

2. Territoriality

Territoriality may be defined as "any behavioral phenomena which effects the exclusion of some category of conspecific organisms from space inhabited by the territorial individual or group" (Anderson and Hill, 1965). There is often a close relationship between territorial behavior and dominance hierarchies. Usually the lowest animal in the hierarchy is last to obtain a territory or might not obtain one at all.

In rhesus monkeys (Maccaca mulata), group territorial range was progressively restricted as the most dominant males were removed from the group (Carpenter, 1958). Group dominance depends on the dominant male and can be reversed by removing him from the group (Marsden, 1968).

The defense of territory often, but not always, involves fighting. In gibbons, territorial ranges are defended both by actual fighting and by vocalizations (Carpenter, 1963). In the monkey Colobus guereza, territorial spacing between group territories is maintained by the roar of the adult males (Marler, 1969). While there is no antagonism within the group territory or coterie of the prairie dog, any animal entering another group's territory is attacked and chased out (King, 1955). Intrusion into another group's den is one of the surest ways of evoking aggression in wolves (Scott and Fuller, 1965). Female wild rabbits are intolerant of other animals near their burrow during the breeding season (Southern, 1948).

There is some question of whether or not house mice defend territories. Young, et. al. (1950) indicate a poor development of territorial behavior in populations of house mice (Mus musculus). On the other hand, Mackintosh (1970) has presented evidence for territory formation in laboratory mice, and Southwick (1955a) observed that an aggressive mouse seems to maintain a small area about him and would attack other mice coming in too close. Male mice attack and drive away any mice intruding into their nest box or an area around it. Correlations between success in fighting and locality suggest that the area defended may be regarded as a territory (Crowcroft, 1955). Whether or not such territorial defense occurs in natural populations is an unsettled question, but Anderson and Hill (1965) have experimentally induced territory formation in Mus musculus by a sequence of events which they hypothesise could occur under natural conditions.

Rats can be considered territorial since newcomers to a colony are attacked and aggressiveness is much greater when a male is in familiar surroundings. Barnett (1958a) does not consider them as having either single or group territories since all acts of defense are performed by single animals acting independently. However, the defended area is occupied by a group. In parturant female rats, the territory coincided with the nest and is defended against colony members as well as strangers (Barnett, 1958a). Although the fighting of male rats is by definition territorial, it evidently depends also on the strangeness of the animal attacked, and usually strangeness in itself is enough to evoke fighting in many animals. Rats which are newly introduced into a colony are attacked and defeated regardless of size; this keeps intruders away.

3. Population Regulation

One of the advantages of territorial behavior is that it can limit population size in a density-dependent manner before such mechanisms as food shortage can take effect (Wynne-Edwards, 1962, 1964). By "density-dependent" it is meant that the "factor is so influenced by population density that it opposes the tendencies of populations to grow with greater intensity at high densities than at lower ones" (Nicholson, 1957). For example, in an experimental rat colony, limitation of population growth occurred as a result of the development of local groups which restricted the utilisation of space (Calhoun, 1952). At low densities, muskrats tend to inhabit only the most favorable habitat, while at very high densities their territories may be spread through the poorer parts as well (Errington, 1951). Survival is probably reduced in these marginal areas. Kluijver and Tinbergen (1953) found evidence that in titmice, territories impose a ceiling on population density. Surplus animals are forced into less favorable habitats where survival and reproduction are probably reduced. Death may occur among animals driven from colonies, herds or packs, or from a suitable habitat (Barnett, 1967b). Such organisms, which "contest" rather than "scramble" for their limiting requisite, eliminate or reduce wastage of that requisite, permitting an optimum density of animals to be maintained. But more important, the violent oscillations in population numbers characteristic of "scramble" competition are avoided. In these instances, when a population reaches a level where it exhausts its means of sustenance, a "crash" will inevitably follow. There are many examples of such catastrophies, particularly among insects (Bates, 1968).

Aggressive behavior can also act directly to limit population size. Species which normally do not experience high densities seem to be more prone to exhibit overt fighting and cannibalism of young when individuals are crowded (Lidicker, 1965). In muskrats, the maximum breeding densities seem to be determined by what the residents will tolerate, the intensity of the fighting, and other manifestations of intolerance. Intraspecific intolerance seems to be a basic mechanism for regulating their numbers (Errington, 1946). Seasonal changes in aggressiveness may also regulate numbers in woodchucks (Bronson, 1963) and in wild rabbits. Southern (1948) found that young bucks decline in numbers after August, and some were observed to be driven out by older ones. Artificial supersaturation of a natural rat population led to a decrease in the size of the population through increased mortality, possibly due to fighting (Calhoun, 1948).

Sadlier (1965) noted that seasonal changes in survival in feral juvenile deermice (Peromyscus maniculatus austerus) were correlated with seasonal changes in aggressiveness of adult males in a laboratory colony. He postulated a causal relationship between these two observations. Healey (1967) confirmed these results and reexamined the relationship between adult aggressiveness and juvenile survival and growth in the field. Juveniles grew poorly when competing with aggressive adults and disappeared rapidly from experimental field plots when the adult population was aggressive. Immigrants were more successful in establishing themselves on trapped-out plots. From his observations, Healey suggests that the social unit in deermice consists of an animal and its neighbors. Antagonism is reduced but individuals remain aggressive and intolerant of strangers, which prevents immigrants from settling. Thus juveniles driven away by aggressive males cannot establish themselves and probably die unless there are uninhabited territories available. This places a ceiling on population size. Chitty (1952) has also noted a high death rate among young field voles (Microtus agrestis) at high population densities during the breeding season. He suggests that this is a direct result of fighting.

Another way in which aggressive behavior can limit population numbers is through high litter mortality. In mice, Christian (1963) noted a marked decline in litter survival with increasing density. In populations of house mice, destruction of litters by killing or abandonment was the most significant block to population growth (Brown, 1953). Southwick (1955a) found that when his mouse populations built up to the point where fighting was observed at a high rate, litter survival was reduced to the point where population growth ceased. This excessive litter mortality is related to intense aggressive activity, the breakdown of female nest defense, disruption of nest building, and general social instability. Calhoun (1962a) also found that stress from social interaction led to such disruption of maternal behavior that few young survived. This perhaps resulted from the abnormal aggressive behavior displayed by certain males such as tail-biting, biting of young, biting during mounting, and slashing attacks which occurred as a result of the "behavioral sink" (Calhoun, 1962c).

Fighting can also act in an indirect fashion to control population growth through its effects on physiology. These changes, some of which will be discussed in a later section, lead to decreased fertility, death during prenatal life, and increased mortality of both young and adult animals.

Reduced fertility and a decrease in the number of pregnancies can result from a variety of causes related to density and to agonistic behavior. First of all, social instability occurring with high density may lead to a situation observed in mice by Southwick (1955b) and in rats by Calhoun (1962b) in which no single male could remain astride a female long enough to complete copulation. Second, estrus cycles may be interfered with and females may even go into periods of prolonged anestrus (Eisenberg, 1967; Chitty and Austin, 1957). Lowered fertility resulting in cessation of reproduction with increasing density has been found in <u>Mus</u> (Crew and Mirskaia, 1931; Crowcroft and Rowe, 1957; Strecker and Emlen, 1953), in <u>Peromyscus</u> <u>maniculatus</u> (Terman, 1965), and in rats (Barnett, 1967b). Bruce (1959) has demonstrated the effectiveness of exteroreceptive stimuli in blocking pregnancy in mice.

Disturbance of maternal physiology can also occur through inanition due to a gradient of availability to food resulting from the type of social organization (Calhoun, 1949). However, cessation of reproduction may occur only in cases of confinement since Strecker (1954) found that with a limited food supply in an unconfined population, the population remained fairly stable without actual food shortage occurring. Excess individuals emigrated from the colony with no indication of a change in rate of reproduction within the colony. On the other hand, in a confined population, limited food supply resulted in abrupt cessation of reproduction (Strecker and Emlen, 1953).

Increased density and disturbance of social behavior may also result in curtailment of population growth through increased resorption of embryos (Helmreich, 1960; Christian, 1958), death of near-term fetuses, and even death of females during pregnancy (Calhoun, 1963).

These alterations of maternal physiology not only curtail growth of the populations in which they occur, but may alter the physiology of full-term offspring for future generations. Christian and Le Munyan (1958) showed that offspring nurtured by previously crowded mothers weighed less than controls and that this effect persists for at least two generations. Chitty (1952) reported that poor survival of young _Microtus spp._ born in populations of high density could not be attributed to environmental conditions. He postulated that prolonged physiological changes in females resulting from fighting leads to abnormalities of the offspring. Attainment of sexual maturity of house mice is delayed at high densities (Christian, 1958). Chitty (1957) hypothesizes that antagonism associated with high breeding density brings about a genetic change in the contemporary population and subsequent generation which become less resistant to the normal forces of mortality.

The Measurement of Fighting Behavior

Several methods have been employed to evaluate fighting behavior. In the round robin technique devised by Seward (1945) each animal meets each other animal for a fixed length of time. The dangling technique employed by Bauer (1956) permits some control over the stimulus since one animal is held by the tail. Levine (1959) used fighting response latency as a measure of aggressiveness, and number of attacks and fight outcome (Levine, et. al., 1965). Catlett (1961) reported accumulated attacking time to be superior to latency and number of attacks. A number of scales of aggressiveness have also been employed. In these instances animals are rated according to the criteria of the particular scale (Davis, 1933) or matched against animals whose aggressiveness relative to one another is known (Sadlier, 1965; Healey, 1967). Aggression may also be measured in terms of its effect, e. g. wounds (Scott, 1966). Several researchers have also devised competitive techniques for evaluating aggressiveness (Fredericson, 1950; Lindzey, et. al., 1961).

Factors Affecting Fighting Behavior

1. Stimuli for Fighting

In discussing the numerous factors which qualitatively or quantitatively affect fighting behavior, it is useful to distinguish short-term from long-term factors. Among the short-term factors, several stimuli have been identified as effective in eliciting fighting in animals.

Hunger causes animals to become more aggressive. Food deprivation was found to reduce the latency to fight in mice (Fredericson, 1950) and to increase aggressiveness in rats (Barnett, 1967a). Collias (1944) suggests that hunger increases aggression by inhibiting fear to some extent. Animals which do not ordinarily fight will fight in a food competition situation (Fredericson, 1952). Indian rhesus monkeys inhabiting urban areas are much more aggressive than forest dwellers of the same species. Singh (1969) believes that this is related to the competition accompanying the limited availability of food in the urban environment. Once the fighting habit is well established, food fails to be an effective stimulus, and trained fighters deprived of food will fight instead of eat (Kuo, 1960).

Although animals such as baboons, dogs, deer, and mountain sheep fight over females, male mice and rats do not appear to fight over mates _per se_ (Scott, 1958). The presence of females, however, does affect the fighting behavior of males. Ginsburg and Allee (1942) reported that the presence of a female stimulates fighting and successful defense of a home cage in otherwise passive male mice. On the other hand, the presence of a female delays or decreases spontaneous fighting in certain strains of mice but has no effect on others (Fredericson, _et_. _al_., 1955; Levine, _et_. _al_., 1965a). Wild rats (_Rattus norvegicus_) attacked strange males more frequently in the presence of females than in their absence (Barnett, _et_. _al_., 1968). There is also more fighting between males in mixed than in all-male colonies (Barnett, 1963).

Fighting can be elicited as an unconditioned response by a variety of aversive stimuli such as foot-shock, heat, physical blows, intra-cranial stimuli (Ulrich, 1966; Hutchinson, et. al., 1965), and discontinuing positive reinforcement (Thompson and Bloom, 1966). In fact, the fighting response interferes with avoidance training in paired animals (Ulrich, et. al., 1965).

Blinding does not seriously interfere with the fighting behavior of male mice (Uhrich, 1938). Lagerspetz (1964) found that mice which behave very passively evoke relatively little aggression. The movement of the opponent acts as a stimulus for attack. Flory, et. al., (1965) reported that rats with visual impairment demonstrated less fighting after foot-shock than those with unimpaired vision.

Among other stimuli which make fighting highly probable in many species are the presence of a strange animal and an adult male entering a region in which another adult male is already established. The "home cage effect" in which the resident dominates, has been reported by several authors (Ginsburg and Allee, 1942; Uhrich, 1938, 1940; Davis, 1933).

2. Experiential Factors

The experience of an organism begins before birth, and certain authors have looked at the effects of prenatal experience on subsequent behavior of animals. Thompson (1957) found that offspring of rats exposed to emotional trauma during gestation were more emotional than controls, as measured by activity and latency in leaving the cage. Kahn (1954) subjected pregnant and lactating mice to severe defeat, but his results on the behavior of the offspring were inconclusive. Uyeno (1960) selected for dominant and submissive rats and crossfostered their offspring. Animals born to dominant parents and reared by dominant mothers were less dominant than those reared by submissive mothers. On the other hand, the foster mother's behavior produced no differences in offspring born to submissive parents. Rats handled in infancy are more aggressive than non-handled rats which are prone to "freezing" (Levine, 1959, 1960).

Almost any type of behavior can be produced by varying the developmental circumstances of an animal. Scott and Fredericson (1951) applied the term "passive inhibition" to the observation that by not fighting under certain circumstances, the animal apparently learns not to fight. Kuo (1960) has produced peaceful interspecific coexistence by rearing animals thought to be natural enemies together from an early age.

Mice trained to fight show a decreased latency from trial to trial (Fredericson, 1949). Moreover, defeats tend to decrease, victories to increase the level of aggressiveness in these animals (Lagerspetz, 1961; Ginsburg and Allee, 1942). On the other hand, Seward (1945, 1946) reported a decline in the number of aggressive acts within a ten minute test period from fight to fight, and a decreased tendency to initiate aggression for both winners and losers.

Pre-test experience is also important in determining the outcome of a match. Bevan, et. al. (1960) found that pre-test experience in dominating an escape platform was more important than androgen level in competitive avoidance of shock. Rats given experience in killing mice chose the arm of a maze leading to a mouse while those with no mouse-killing experience chose the arm leading to a rat pup (Myer and White, 1965).

One of the most often investigated variables affecting fighting behavior is that of early social experience. Not unexpectedly, the results vary considerably from study to study. It is essential to bear in mind that contradictory results are largely attributable to differences in species and strains and to differences in experimental design.

Several researchers have reported that social isolation is a primary factor in producing fighters (Kuo, 1960). Mice which are regularly submissive often become aggressive if they have been kept isolated (Ginsburg and Allee, 1942). In the two strains studied, the fighting tendency in communally reared mice was less than if they were reared in isolation. Levine, _et_. _al_. (1965b) found mice housed with the opposing strain for one week prior to testing to be less aggressive than those kept isolated from weaning. Rats isolated for long periods become more nervous and show an increased tendency to bite than those reared in community cages (Wiberg and Grice, 1963). Pairs of rhesus monkeys with restricted social experience showed more frequent and prolonged fighting than feral pairs (Mason, 1960).

Bauer (1956), using the tail-dangling technique, found no differences in fighting for isolated and paired animals, but the frequency of other behavior patterns differed. King and Gurney (1954) observed that males raised with other males had a lower fighting latency than those reared alone. They attributed this to their greater experience, and consequent latent learning, in competing for food and water in the social situation. Pain-elicited fighting appears more frequently in communally reared than in isolated animals (Hutchinson, _et_. _al_., 1965; Ulrich, 1966).

Differences in the level of aggressiveness may be a secondary effect of other modifications of behavior resulting from rearing conditions. For example, rats allowed postweaning contact with the mother or with peers weighed more, displayed more "social-seeking" behavior, and were less "emotional" than isolates (Singh and Maki, 1968). Mice reared in isolation tend to be less investigative than those reared with the mother and siblings (Kahn, 1954). Terman (1963) studied the spatial distribution of released prairie deermice with the result that those raised in isolation combined with the others less and were more affected in their spatial distribution by alien mice than those raised in groups. After three generations of selective breeding, Lagerspetz (1961) found the descendants of aggressive mice to be less reactive emotionally (in defecation and ambulation) than the third generation of non-aggressive mice.

3. Genetic Factors

That the genetic constitution of the organism plays a part in determining its tendency to fight is evidenced by both strain differences and sex differences in fighting behavior. Sex differences will be discussed later. [See pp. 22 - 25]

Ginsburg and Allee (1942) reported definite strain differences in level of aggressiveness between three highly inbred strains of mice as determined by the outcome of fights. C57/Bl mice were superior to C3H agouties which were superior to C albinos. Beeman (1947) also found C57's to fight more frequently than Bagg albinos. Bauer (1956) observed significant differences in several behavior patterns, including frequency of attacks, between C57, Bl/10, and BALB/c mice. The behavior patterns involved in fighting (e.g., eye-closing, tailrattling) of these same strains differ quantitatively (Fredericson, et. al., 1955). CBA males were found to be superior fighters to St albinos in attack latency, number of attacks, and proportion of victories (Levine, et. al., 1965a, 1965b).

The dominance scores of rat offspring of dominant parents were significantly larger than those of submissive parents regardless of whether the foster mother was dominant or submissive (Uyeno, 1960). BALB/c mice show peaceful behavior in a food competition situation while C57's are incapable of sharing a single piece of food. However, when these two strains were paired with each other, eight out of ten of the BALB/c males killed their C57 partner (Fredericson and Birnbaum, 1954). This points out that the outcome of an experiment depends in part on the measurement chosen to test for aggressiveness.

Breed differences in behavior have been studied in dogs. In litters of two breeds reared together, a straight-line dominance order was found with terriers dominant over all of the beagles (James, 1951). Fuller (1953) reported that "ganging up" behavior appears with different frequency in different breeds of dogs; fox terriers "gang up" more often than other breeds studied. Pawlowski and Scott (1966) observed that four breeds of dogs differed markedly in dominance in competition over a bone.

4. Other Factors

There are other important variables which affect the fighting behavior of animals. Nutritional state is very important, and Kuo (1960) found that thiamine and protein improve the fighting ability of Japanese grey quails. Weight can also influence success in fighting. In rat colonies, for example, there was no instance in which a rat defeated a colony member much larger than itself (Barnett, 1963). Pain-elicited fighting increases with age in rats (Ulrich, 1966; Hutchinson, _et_. _al_., 1965).

A radical change in the environmental condition in which an animal is placed tends to abolish a fighting habit previously formed in quails, but not in dogs or Siamese fighting fish (Kuo, 1960). Fighting behavior can also be conditioned classically to a tone stimulus (Vernon and Ulrich, 1966) and as an operant where it undergoes extinction in the absence of the primary reinforcer (Ulrich, _et_. _al_., 1963).

The Physiology of Fighting

As with any behavior pattern, aggression and fighting affect and are in turn affected by physiological changes. Among the most important physiological changes are respiratory rate, blood pressure, blood flow, and hormone levels.

Cannon (1929) first described the "fight or flight" reactions mobilized by adrenalin in which respiration deepens, the heart beats more rapidly, arterial pressure rises, and blood is shifted from the digestive tract to the heart, CNS, and the skeletal muscles. At the same time sugar reserves are released from the liver, the spleen contracts and discharges blood corpuscles, and blood coagulation is hastened. These reactions were produced in cats with the expression of pain, fear, and rage.

The adrenal medulla produces noradrenalin as well as adrenalin. These two hormones are associated with different emotional states.

Anxiety is accompanied by noradrenalin production whereas aggressive states are characterised by adrenalin (Klopper, 1964). In humans, Funkenstein (1955) reports that anger directed outward is associated with the secretion of noradrenalin, while depression and anxiety are associated with adrenalin. These secretions result from stimulation of different areas of the hypothalamus. The hypothalamus contains relatively high concentrations of both noradrenalin and adrenalin, and there is evidence of central adrenoreceptive mechanisms in the hypothalamus (Klopper, 1964). While adrenalin is produced during fighting, it apparently cannot produce the aggressive state. Allee and Collias (1938) were not able to change the social position or aggressiveness of hens by injecting them with adrenalin. However, Siamese fighting fish (*Betta splendens*) display significantly more fin extensions and gill flaring responses with norepinephrine bitartrate solutions in their water (Marrone, *et*. *al*., 1966).

Two groups of adrenocortical hormones are also involved in the physiology of aggression, cortisone and corticosterone. In acute aggression the output of cortical hormones rises, probably as a consequence of release of ACTH from the pituitary. The relationship between aggression and other psychosocial factors and cortical hormones is a complicated one and will be discussed in detail in a later section.

Different physiological mechanisms appear to be involved in preparation for fighting and actual fighting. In cats, preparation for fighting is associated with decreased cardiac output and vasoconstriction in the mesenteric and iliac beds. During fighting, heart rate, cardiac output, and total peripheral conductance increase, and there is dilation of the iliac bed. Blood pressure is high in both instances but different mechanisms are involved in its maintenance. In addition, cardiovascular changes during naturally elicited preparation for fighting are different from those obtained from electrical stimulation of the hypothalamus in anaesthetized animals (Adams, et. al., 1968).

Additional physiological reactions occurring upon exposure to attack in rats are lowering of liver glycogen and raising of blood glucose level (Barnett, et. al., 1960). Death may occur from "social stress" with only superficial wounding and without pathological signs on post mortem examination (Barnett, 1958b, 1967b). This may be related to a syndrome called "shock disease" by Green, et. al. (1938, 1940) which reportedly reached epidemic proportions during a period of high density and led to decline in numbers of snowshoe hares (Frank, 1957). No pathogen was found; the condition was characterized by degeneration of the liver, failure to store glycogen, and low blood sugar level. Death occurred from hypoglycemic shock. Frank (1957) claims that hypoglycemic shock is a significant mortality factor in populations of Microtus arvalis. These physiological effects may be explainable in terms of the "general adaptation syndrome" (GAS) postulated by Selye (1946). [See p. 139]

Another physiological factor that has a significant effect on fighting behavior is sex hormones. Evans (1936) reported that removal of the ovaries in female lizards (Anolis carolinesis) results in increased aggressiveness and the tendency to defend a territory. Injection of low-ranking hens with testosterone proprionate caused them to rise in the social order by markedly increasing their aggressiveness (Allee, et. al., 1939). Beeman (1947) castrated two strains of mice both as juveniles and as adults and found that they failed to display aggressive behavior. Testosterone therapy increased the aggressive level of the castrates. Bevan, et. al. (1957) found that non-castrates fought twice as frequently as castrated mice, and that castrates receiving hormone therapy were superior in fighting compared to non-treated animals. However, using three dosages of testosterone, none of the operated group approached the level of aggressiveness of unoperated mice (Bevan, et. al., 1958).

Mice do not normally fight before thirty-four days of age but they can be induced to fight as early as eighteen days when injected with testosterone (Levy and King, 1953). Both male and female chicks treated with gonadal hormones formed peck orders somewhat earlier than did untreated chicks. Androgen treatment caused an increase in aggressiveness whereas estrogen treatment led to increased submissiveness (Guhl, 1961). Castration also reduces the probability of fighting in response to foot-shock in adult rats (Hutchinson, et. al., 1965).

Indirect evidence for the importance of the male hormone comes from studies which have demonstrated the seasonal nature of aggressive behavior related to the breeding season in woodchucks (Bronson, 1963) and in *Peromyscus* (Sadlier, 1965; Healey, 1967). But how does testosterone alter fighting behavior? It is well known that there are sex differences in many aspects of agonistic behavior. Levine (1966) has suggested that gonadal hormones may determine sexual differentiation of the brain in the first few days after birth. This may produce a permanent change in the sensitivity of the brain to sex hormones. The incidence of spontaneous aggression in adult male mice injected with a single dose of estradiol benzoate at three days of age was less than that of oil-injected controls (Bronson and Desjardins, 1968). Kuo (1960), who found that male sex hormones enhance fighting in quails, raises the question of whether this is through enhancement of virility as is the case with nutritional factors. Whatever the mechanism, male hormones somehow affect a lowering of the threshold for fighting in many animals.

As was pointed out earlier, females of several species display a significant amount of aggressiveness. In the phalarope, the male and female roles are partially reversed. The female is more colorful, more active in courtship, and more aggressive than her partner. Hohn (1969) reported that the concentration of androgens is greater in the ovaries than in the testes in this species. Female hamsters are also more aggressive than males; a male will almost invariably be attacked when the female is not in estrus. Ovarectomized hamsters are continuously aggressive, although somewhat less so than intact animals in diestrus. Estrogen therapy followed by a single injection of progesterone brings castrated females into heat, eliminating fighting (Kislak and Beach, 1955). Prolactin also affects parental and fighting behavior of females.

Uhrich (1938) noted that castration does not completely inhibit fighting in all individuals. Castrated male swordtail fish (Xiphophorus) apparently maintain their social position for one to six and a half months after castration (Noble and Borne, 1940). Beeman (1947) noted that the cessation of fighting depended on whether castration was performed before or after pre-test training. In either case, pre-fight experience was more important than the androgen status of the animal in determining the winner in a competitive avoidance situation (Bevan, *et*. *al*., 1960).

The Gerbil as an Experimental Animal

Since the Mongolian gerbil (*Meriones* *unguiculatus*) is a relatively new experimental animal, it is worthwhile to review briefly some of the work that has been done with them. Gerbils comprise three genera of the rodent family Cricetidae: *Gerbillus*, *Tatera* and *Meriones*. Thomas (1919) listed eight species in the genus *Meriones*, but in 1947 Chaworth-Musters and Ellerman revised the genus and listed eleven species, including *unguiculatus*. Walker (1968) lists twelve species of *Meriones* and cites the correct common name of *M*. *unguiculatus* as the black-clawed jird.

Meriones *unguiculatus* inhabits the dry sandy areas of eastern Mongolia, northern China, and western Manchuria. They are active both day and night, live in colonies, and have underground burrow systems with nest and food-storage areas. They reportedly breed all year (Tanimoto, 1943). Other than these few observations and those made by Won (unpublished data) on their tunnels, breeding, diet, postnatal development, and distribution, there is no information on their ecology or behavior in their natural habitat. There is, however, some information available on closely related species (Bodenheimer, 1949; Prakash, 1959, 1962; Purohuit, 1967; Garbuzer, *et*. *al*., 1968).

Schwentker has compiled an annotated bibliography and manual on the care and maintenance of *M*. *unguiculatus* (both available from Tumblebrook Farm, Brant Lake, N. Y.). Physiological studies have been made on their water balance (Winkelmann and Getz, 1962; Kutscher, 1968; Kutscher, *et*. *al*., 1968), temperature regulation (Robinson, 1959), reproduction (Marston and Chang, 1964, 1965; Nakai, et. al., 1960; Barfield and Beeman, 1968), and resistance to radiation (Chang, et. al., 1964).

An interesting and unique anatomical structure, the midventral sebaceous gland has been described in M. unguiculatus (Webster, 1963; Mitchell and Feldman, 1966; Feldman and Mitchell, 1968). The effects of castration and of gonadal hormones on its development and activity have been investigated (Arluk, 1966, 1969; Thiessen, Friend, and Lindzey, 1968; Lindzey, et. al., 1968). Thiessen and his co-workers (Thiessen, et. al., 1970: Thiessen, Friend, et. al., 1968) have investigated the role of hormones and environmental structure on the abdominal skimming response. Mitchell (1967) reported that this gland is not necessary for reproduction, and others have suggested a possible role in territorial marking (Sokolov and Skurat, 1966; Thiessen, Friend, and Lindzey, 1968).

Several studies have been made on various aspects of the behavior of M. unguiculatus. Walters, et. al. (1963) and Glickman and Hartz (1964) have described their exploratory and avoidance behavior. Boice, et. al. (1968) compared their reaction to shock with that of kangaroo rats and mice, while Nauman (unpublished data) has compared their behavior in an open field with that of rats. Weckin (1969) has studied competitive avoidance and food competition. Glickman, et. al. (1967) studied shredding of nest material by this species. Investigations have been made on visual behavior (Routenberg and Glickman, 1964; Blum, et. al., 1967; Thiessen, Lindzey, et. al., 1968; Reese, personal communication), maze running behavior (Webster and Caccavale, 1966), reproductive behavior (Marston and Chang, 1965; Kuehn and Zucker, 1966; Barfield and Beeman, 1968), and activity rhythms (Mizell, et. al., 1968). "Thumping" or "foot-stomping" is a behavior pattern involving rhythmic and repetitive lifting and lowering of the hind feet. Gerbils have been observed to do this during mating activity (Kuehn and Zucker, 1968) and after cessation of rewarding brain stimulation (Routtenberg and Dramis, 1967). They are also prone to epileptiform-type seizures which have been described by Friend, et. al. (1967), Thiessen, Lindzey, and Friend (1968), and Nauman (1963). These seizures occur during handling, cage changing, and upon exposure to a variety of novel stimuli.

Scope of the Present Study

The Mongolian gerbil is a convenient animal to work with, and my preliminary observations indicated a large individual variability in their tendency to fight. This offered the opportunity to examine some of the variables affecting fighting and related social behavior in this species. Although the literature on aggressive behavior in rodents is extensive, it is valuable to extend studies of fighting behavior to species other than mice and rats so that certain generalizations might eventually be deduced. Furthermore, M. unguiculatus exhibits certain qualitative differences from these species in its fighting behavior, particularly in the high level of female aggressiveness.

The few studies that have examined their social behavior have reported gerbils to be relatively nonaggressive (Nauman, 1963; Eisenberg, 1967; Fisler, 1969). But Nauman (1963) has observed fighting and has suggested that it is territorial in nature.

During preliminary observations of social behavior, I often, but not always witnessed fighting. This raised interesting questions about the conditions necessary to bring about a fight. The present study was designed to investigate some of the factors which could influence fighting and related aspects of social behavior. Some of the questions posed were: Does early and prolonged social deprivation produce a more aggressive gerbil? Can differences in fighting behavior between isolated and group-reared animals be correlated with differences in other aspects of social behavior? Did the gerbil's sex affect its tendency to fight. My earlier observations had indicated that females fought at least as often as males, so it seemed worthwhile to investigate fighting in females since it had been overlooked so often in studies of other species. Finally, were there differences in behavior if an animal met another in his own cage as opposed to meeting in a "neutral" cage? Several of the authors cited above found a distinct "home cage effect" in fighting success and attributed this to territoriality. A more parsimonious explanation for this effect might be found by examining a wider range of behavior patterns.

Another object of this study was to investigate social behavior in a population situation within an area considerably larger than a cage. While it is impossible to study a natural population under laboratory conditions, a population confined in a relatively large area would give more information about the social structure of this species than could be learned with animals in small cages. The major questions posed here were: (1) What is the effect of density on fighting and other forms of social behavior? (2) Do gerbils form social hierarchies? (3) Are they territorial? (4) Would the initial size of the population affect the size at which it leveled off, or is there some kind of density-dependent mechanism of population regulation?

Finally, an attempt was made to assess the effects of fighting and density on the physiology of *M. unguiculatus*. The weight of the adrenals, spleen, and parts of the male and female reproductive tracts were recorded as indirect measures of their activity. These organs were selected because they are the ones most often implicated in studies on stress and density.

METHODS AND MATERIALS

Paired Matches

Sixteen pregnant gerbils were obtained from Tumblebrook Farm, Brant Lake, New York. Each was caged in a screen-covered ten gallon aquarium. Wood shavings and cotton were provided for nest material. Rockland mouse-rat diet and water were available ad libitum, and fresh vegetables were given twice a week. All litters were born within a one week interval.

The pups were weaned at twenty-five days of age and placed either individually or in unisexual groups of five in similar ten gallon aquaria. These were painted black on two sides so that animals in adjacent cages were visually isolated from one another. Only gerbils from litters of five to seven were used in this part of the study. Each litter was split so that some individuals were placed in groups while others were isolated.

A total of fifty grouped animals, twenty-five males and twenty-five females, and thirty individually-reared gerbils, eighteen females and twelve males were obtained in this way. These animals were maintained on the same diet as their mothers, except for supplementary rolled oats supplied for the first few weeks after weaning. The arrangement of paired matches eliminated the need for one group-reared male and one group-reared female. As several animals died before the conclusion of the study, only the data for those animals that completed the scheduled sequence were analyzed. This included twenty-four "grouped" females, twenty "grouped" males, eighteen "isolated" females, and ten "isolated" males.

The gerbils were maintained as described above until they were approximately eight months old. During this time they were handled only for ear-punching, cage changing, weighing, and once for fur-clipping one week prior to the initiation of the experiments. Between the ages of eight and ten months their behavior was observed as follows.

Individuals were paired with strange animals of the same sex and social experience. Matches were arranged in such a way that half of all first matches were in one gerbil's home cage, and the other half were in a neutral cage with clean wood shavings. The four cage-mates of each group-reared animal were removed before each home cage match. In the second encounter, which took place ten to fourteen days after the first, the sites were reversed so that animals that had met in a neutral cage now met in a home cage, and vice versa. All third matches were in the home cage of animals which had previously met in another's cage. Thus, each gerbil was involved in three matches, one in its own cage, one in another gerbil's cage, and one in a neutral cage. The matches scheduled for a single day included each of the four groups (i.e., group-reared females, group-reared males, isolated females, isolated males) and were arranged so that no group met consistently at the same time of day.

The experimental situation consisted of placing the two opponents in the appropriate cage, separated by an opaque partition. The "home" animal was lifted in the same manner as the other animal. After three minutes the partition was removed and the animals were observed through a one-way mirror for twenty minutes.

A recording system, similar to one described by Tobach, et. al. (1962), was designed and built for this study. The keyboard (Plate 1) consists of eighteen keys and eighteen switches. With a given switch in the manual position, depression of the corresponding key produces a single record. When the switch is in the latched position, the key records repeatedly, until it is again depressed. The keyboard provides for data accumulation periods of several lengths; in these experiments the period used was one second. Therefore, anytime two or more keys were pressed within a one-second interval, they were recorded synchronously. The keyboard is also equipped with a digital time-keeping device which records the total number of accumulation periods. Since a one-second accumulation period was employed, the clock recorded the elapsed time, in seconds, from the beginning of each match. An eight-channel paper tape punch (series 110, Ohr-tronics, Inc., Montvale, N. J.) was activated by the keyboard. This was placed in a closet about twenty-five feet from the observation area, and an air conditioner and two fans provided a source of "white" noise so that the animals would not react to the sound of the tape punch.

The data recorded before each match were: (1) time of day; (2) relative humidity; (3) match number 1, 2, or 3 for the participating animals; (4) identification numbers of the animals; (5) rearing conditions; (6) sex; (7) which gerbil was heavier; and, (8) the cage employed. Temperature was maintained at a constant 19-20° C.

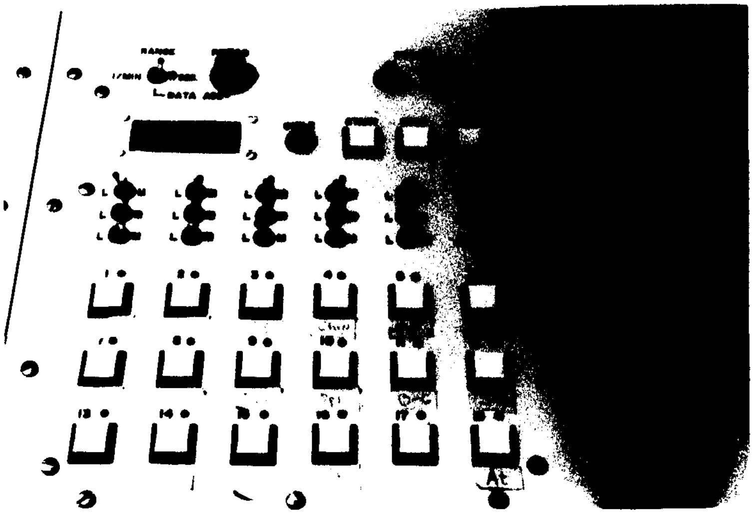


Plate 1. Keyboard

Plate 2. Nosing

Behavioral Patterns Recorded

The following behavioral patterns were recorded by depressing appropriate keys (not necessarily corresponding to the number below) as the behavior occurred. Another key was depressed along with each behavior key to designate which animal was involved.

1. Mounting -- climbing on the back with forefeet in contact with the other animal. No sexual connotation is implied.
2. Foot-stomping -- a rhythmic and repetitive lifting and lowering of the hind legs in one place. Forefeet may or may not be in contact with the substrate.
3. Nosing -- placing the nose in contact with the other animal's nose (Plate 2).
4. Chinning -- placing the nose to the chin of the other animal (Plate 3).
5. Investigating the midventral gland -- placing the nose on the midventral gland of the other animal.
6. Investigating the genitalia -- placing the nose on the anal-genital area of the other animal (Plate 4).
7. Grooming -- active licking of the other animal's fur. If items 4, 5, or 6 were recorded with this behavior pattern, this would designate the area being groomed.
8. Self-grooming -- scratching or licking any part of the gerbil's own body. If item 6 was also scored, this indicated that the animal was grooming its anal-genital region (Plate 5).
9. Boxing -- both animals in an upright position facing each other. Forefeet are usually in contact with one another (Plate 6).

Plate 3. Chinning

Plate 4. Investigating the genitalia

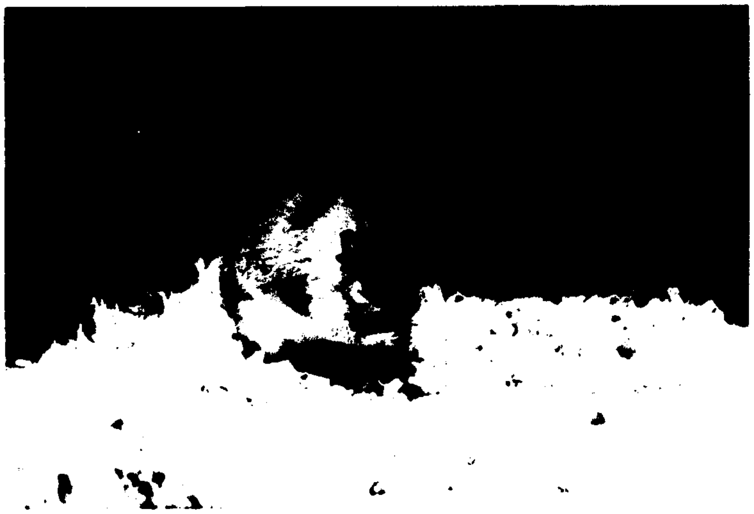


Plate 5. Self-grooming

Plate 6. Boxing

10. Approaching -- one animal moving directly toward the other. This was not scored if the animal encountered the other while moving randomly around the cage.

11. Skimming -- the animal flattens out and pulls itself forward, dragging the abdomen along the substrate (Plate 7).

12. Sniffing -- moving the nose across any area of the body of the other animal except those regions designated by other keys. This was scored each time the nose was visibly moved (Plates 8 & 9).

13. Defense -- the animal is in a semi-upright position and extends its forefeet and nose towards the head of the other animal. Usually the forefeet are pressed against the other's head and the nose is close to its ear (Plates 10 & 11).

14. Hipping -- this posture is characteristic of an attacking animal prior to attack. The back is arched, there is pilo-erection of the fur, the eyes are narrowed, and the hip is pressed against the side of the opponent. A great deal of movement often accompanies this posture (Plates 12, 13, & 14).

15. Digging -- the animal digs at the substrate or scratches at the floor or walls of the cage. This was often accompanied by a backward kick of the material accumulated under the hindfeet.

16. Attacking/Fighting -- this involves all forms of actual physical combat including biting, kicking, and wrestling. The distinction between fighting in which both animals actively participate, and attacking, involving only one animal, was made by means of the keys designating which animals were involved.

A direct read-out of the data on the paper tape was provided by an appropriately programmed PDP-8 computer (Digital Equipment

Plate 7. Skimming

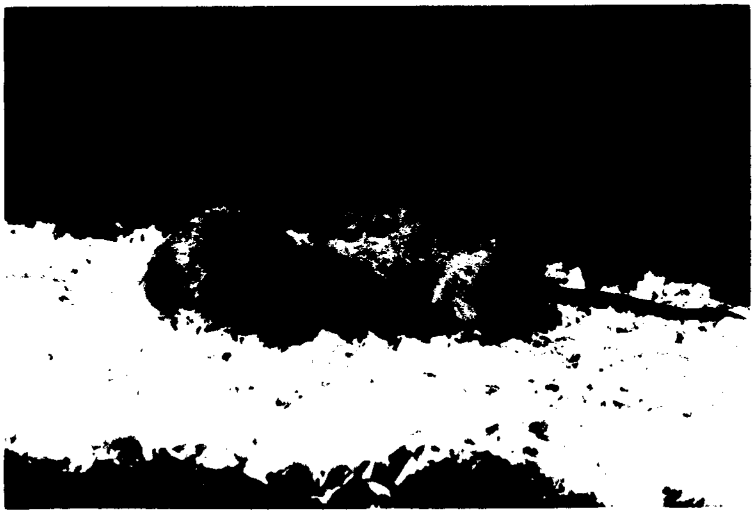


Plate 8. Mutual sniffing

Plate 9. Uni-directional sniffing

Plate 10. Defense

Plate 11. Defense (gerbil on left)

Plate 12. Hipping (gerbil in foreground)

Plate 13. Hipping, rear view

Plate 14. Hipping accompanied by movement

Corporation, Maynard, Mass.). Tallying was done by hand, and the statistical tests were performed with the use of a Wang 362 calculator (Tewksbury, Mass.).

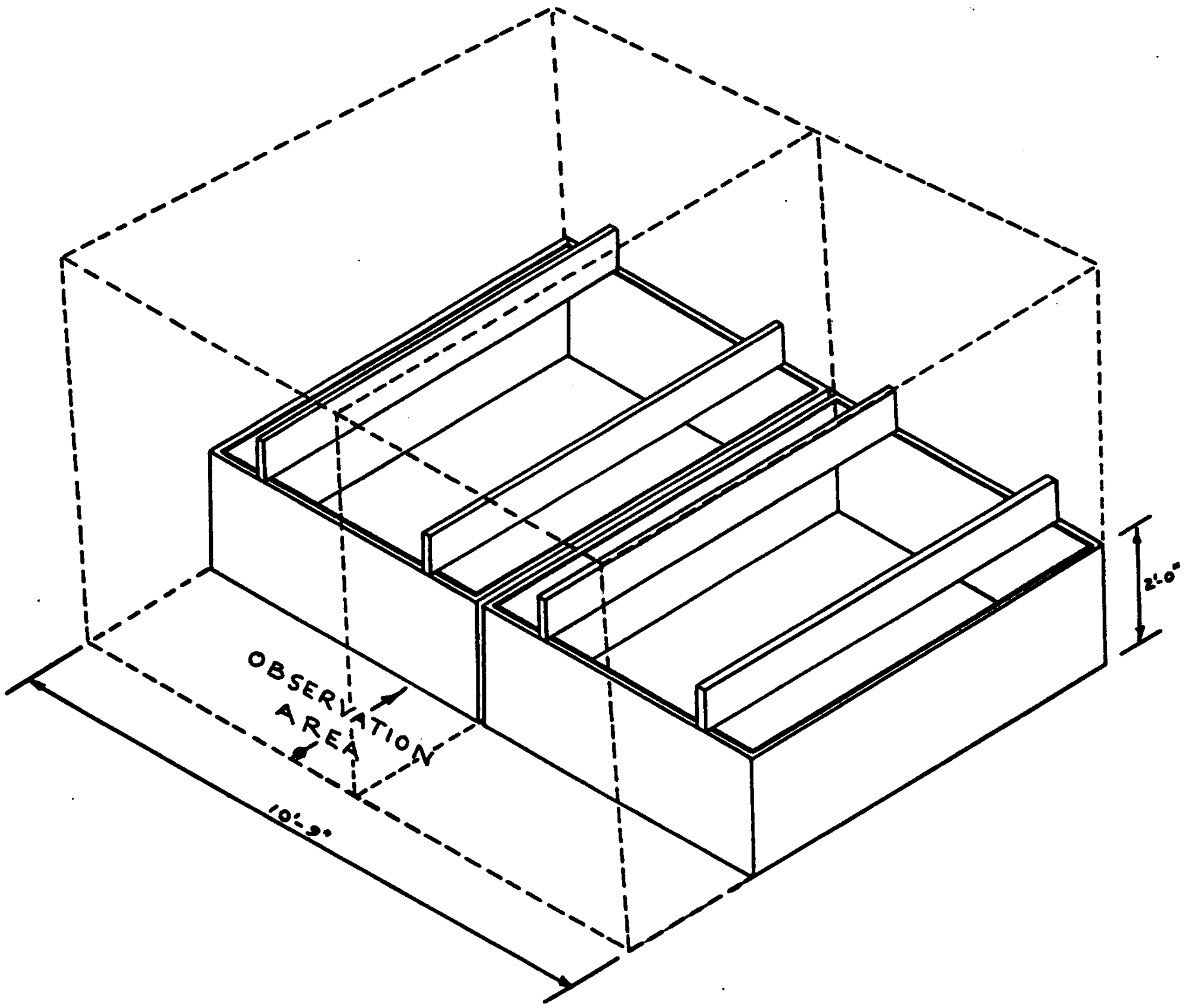
Population Study

Gerbils were placed in two 9 ft. x 5½ ft. enclosures (Figure 1), with linoleum floors covered with wood shavings and cotton. To prevent the animals from climbing out, each enclosure was lined with aluminum to a height of two feet. The pens were enclosed by a wood frame and insulated sheetrock walls. Each has a 5½ ft. x 2 ft. observation area which was separated from the animals by a 2 ft. wall. The enclosures were lit by large fluorescent fixtures regulated on a 12L/12D photoperiod and were ventilated by light-proof fans. Access to each observation area was provided by folding doors.

The original animals used in the population study were adults of known age. They were marked by both ear-punches and fur-clipping which permitted identification and sexing from a distance. Thirty-six gerbils, eighteen males and eighteen females were released into one enclosure and designated the "high density" population. The "low density" population was started by releasing two males and two females into the other enclosure. Both groups were provided with food and water *ad libitum* and given fresh vegetables twice a week.

An average of four observation periods, ranging from thirty minutes to two hours in length, were made per week until no fighting was observed during these periods. The data recorded included the time of day, temperature, relative humidity, all fights, chases, and attacks and the animals involved, nesting locations, and other mani-

Figure 1. Isometric diagram showing the two adjacent population enclosures and observation areas.



ANIMAL PENS

festations of social behavior. Records were kept of all births and deaths and whether injury was involved. Animals were captured once every four weeks when the enclosures were cleaned; they were then weighed and reclipped when possible (badly wounded animals were usually missing too much hair). Post mortems were made on all dead adults unless decomposition was too extensive. The populations were studied for a period of sixteen months.

Physiological Study

About a week following the termination of the paired encounters, the experimental animals were killed with chloroform and their adrenal glands, spleen, and testes or female reproductive tract (ovaries, oviducts, and uterus) were removed. The organs were fixed in 10% formalin and weighed on a Mettler analytical balance at a later time.

Organs from gerbils killed in the enclosures were treated in the same manner, but in this case the animals were dead for varying lengths of time prior to autopsy. If too much autolysis had occurred, they had to be discarded.

Control animals were reared until they were five and a half months old in the same manner as those used in the paired encounters. They were then killed with chloroform and their organs fixed and weighed.

Statistical Methods

In order to choose the appropriate tools for the analysis of the data, it was necessary to determine whether the experimental design introduced biases that would make interpretation of the results difficult. Two such possible confounding factors were the sequence of observation and the variability of subjects within any one rearing treatment group. Because the measures used were most appropriately analyzed by non-parametric techniques (Siegel, 1956), the Friedman Two Way Analysis of Variance was used to determine the effects of sequence. In addition, for the purpose of using group scores rather than individual measurement, each dependent variable was analyzed by the Friedman Two Way Analysis of Variance to determine the variability among members of any group on any parameter. Because of the type of measures studied, the nature of the data obtained, and the statistical characteristics of the data, non-parametric techniques were used to determine group differences and correlations among measures. The specific test is stated as the measure is discussed.

It should be noted that when there were many zero scores for any measure, the precise median was not reported as the "zero" value was sufficiently informative as a median when given with the range.

RESULTS

Paired Matches

The two major factors which had to be analyzed in this part of the study were individual differences among gerbils within a single experimental treatment group and group differences in behavior related to sex and rearing experience. Before group differences can be properly treated, it is necessary to consider the other variables which were introduced as a result of the experimental design. These include the effects of the observational sequence and of the observational cage on the four experimental groups.

1. Individual differences

Analysis of twenty-three measurements of behavior for four groups of gerbils showed that individual differences in behavior reached the level of statistical significance in only three cases (Friedman two-way analysis of variance, Siegel, 1956). As this number might be expected by chance, it was considered that there were no significant individual variations in behavior within each group.

2. Differences related to rearing and to sex

a. Effects of observational sequence only on behavior

As each animal was observed three times, it is necessary to evaluate the effects of the observational sequence on the behavioral measures, regardless of the type of cage used for the observation. The following behavior patterns for the indicated groups were found to differ significantly in relation to the sequence of observation. (see Table 1; see Appendix for complete data).

Approaching: sequence of matches was statistically significant for group-reared males (Friedman, $p < .01$) and group-reared females (Friedman, $p < .01$). For both groups the frequency increased between matches one and three (Sign test, $p < .02$ for females, $p < .05$ for males).

Sniffing: sequence of matches was statistically significant for group-reared males (Friedman, $p < .01$) and individually-reared females (Friedman, $p = .05$). The frequency of sniffing increased between matches one and two (Sign test, $p < .01$) and between matches one and three (Sign test, $p < .05$) for the first group, and decreased from match one to three (Sign test, $p < .05$) for the second.

These significant sequential differences were taken into account in the analysis of group differences in behavior in that all analyses were done within the sequence position. The Kruskal-Wallis one-way analysis of variance (Siegel, 1956) was used in the following group comparisons. A four-way analysis was first done, followed by a two-way analysis between pairs of groups differing in only one variable (i.e., grouped vs. individually-reared and males vs. females).

For these two behavior patterns (approaching and sniffing) in which sequence but not cage was important (see Table 1), there were significant differences among the four groups during the second ($p < .01$ for sniffing; $p < .02$ for approaching) and third ($p < .01$ for sniffing; $p < .001$ for approaching) matches only. For sniffing the only significant differences between pairs of groups appeared between individually-reared males and individually-reared females in which

Table 1. Medians and ranges for behavior patterns affected by observational sequence, but not cage

		Group-reared		Individually-reared	
Behavior pattern	Match No.	Males N = 20	Females N = 24	Males N = 10	Females N = 18
	1	14.5 6 - 37	18 6 - 37	18 8 - 56	14 3 - 37
Approaching	2	21 2 - 43	23.5 0 - 38	16.5 5 - 55	13.5 0 - 43
	3	23.5 11 - 41	26.5 7 - 50	23 12 - 71	9 1 - 79
	1	17 0 - 39	24.5 0 - 48	23.5 0 - 132	18.5 0 - 112
Sniffing	2	35.5 5 - 84	26 11 - 56	31.5 18 - 104	13.5 3 - 85
	3	23.5 6 - 85	28.5 0 - 87	36 10 - 109	6 0 - 67

males exceeded females in both match two ($p < .01$) and match three ($p < .01$), and between group-reared and individually-reared females in which grouped females sniffed more frequently in both matches ($p < .02$). Approaching was also significantly greater few individually-reared males than for individually-reared females in the third match ($p < .05$) and for grouped than for individually- reared females in the third match ($p < .05$).

The behavior patterns which showed no significant sequence effects included fighting (all measures), mounting, grooming, grooming the chin, grooming the midventral gland, grooming the genitalia, self-grooming, self-grooming the genitalia, investigating the genitalia, skimming, defense, hipping, foot-stomping, boxing, and digging.

b. Effects of observational cage only on behavior

One of the most important variables investigated in this study was that of the cage in which the match occurred. The three observational situations included a neutral cage, a home cage, and the home cage of another animal (other-home).

1) Intra-group cage effects

Table 2 shows the medians and ranges for four measures of fighting behavior for the experimental groups in the three situations. These measures were not affected by sequence of observation.

The cage in which the match occurs is a significant determinant of fighting by all four criteria for group-reared females (Friedman, $p < .02$ for latency and number of fights and attacks; $p < .05$ for time spent fighting) and for group-reared males (McNemar Test, Siegel, 1956). The behavior of individually-reared males and females was not statis-

Table 2. Median and ranges for four measurements of fighting behavior in four groups of gerbils

Group	N	Cage	# of fights	# of attacks	Time spent fighting (sec)	Fight latency (sec)
Grouped males	20	Home	0	0	0	c.b.d.*
			0 - 26	0 - 26	0 - 77	61 - n.f.**
	20	Other	0	0	0	c.b.d.
			0 - 26	0 - 5	0 - 77	88 - n.f.
	20	Neutral	0	0	0	c.b.d.
			0	0	0	n.f.
Grouped females	24	Home	1.5	0	4.0	1068
			0 - 25	0 - 25	0 - 76	22 - n.f.
	24	Other	1.5	0	4.0	1068
			0 - 25	0 - 25	0 - 76	22 - n.f.
	24	Neutral	0	0	0	c.b.d.
			0 - 10	0 - 10	0 - 47	313 - n.f.
Individually-reared males	10	Home	0	0	0	c.b.d.
			0 - 6	0 - 4	0 - 18	139 - n.f.
	10	Other	0	0	0.5	448
			0 - 17	0 - 7	0 - 165	139 - n.f.
	10	Neutral	2.0	0	8.0	517
			0 - 14	0 - 14	0 - 119	32 - n.f.
Individually-reared females	18	Home	6.0	3.0	44.0	412
			0 - 88	0 - 22	0 - 140	1 - n.f.
	18	Other	6.0	1.5	44.0	412
			0 - 88	0 - 88	0 - 140	1 - n.f.
	18	Neutral	12.0	1.0	71.0	278
			0 - 54	0 - 54	0 - 150	2 - n.f.

*c.b.d. = cannot be determined
**n.f. = no fight; total observation = 1200 sec

tically differentiated as to type of observational situation. The significant differences in fighting were as follows (Sign test, Siegel, 1956):

Group-reared females: the total number of fights ($p < .05$) and the amount of time spent in fighting ($p < .05$) were significantly greater in other-home than in neutral cages, while the fight latency was shorter in other-home than in neutral cages ($p < .05$). There were also more attacks ($p < .05$) and a lower fight latency ($p < .05$) in home than in neutral cages. There were no significant differences in fighting behavior between animals in home and in other-home cages.

Group-reared males: the number of fights ($p < .01$), number of attacks ($p < .02$), and total fighting time ($p < .01$) were greater in home than in neutral cages, and the fight latency was lower ($p < .01$) in home than in neutral cages. The number of attacks ($p < .05$), number of fights ($p < .02$), and time spent fighting ($p < .02$) were also greater in other-home cages compared to neutral cages, while the fight latency was shorter in other-home cages ($p < .02$). Again there were no significant differences between the behavior of the animals when in their own and in another animal's home cage.

Comparisons of animals in their own home cage and in another animal's cage (Table 2) reveal no significant differences in the level of aggressiveness between resident (home) and introduced (other-home) animals, as defined operationally by the four measures of fighting behavior used. Therefore, the increase in the amount of fighting apparent for group-reared gerbils in a lived-in cage (i.e., some animal's home cage) compared to that in a neutral cage, suggests that the question of attack initiation and "victory" should be investigated.

Table 3 reveals that there is no significant difference in attack initiation between resident and introduced animals (Chi^2 Test). Table 4 shows the frequency with which resident and introduced animals win, as determined by which animal is the last to attack during the match. Again, residents win slightly but not significantly more often than introduced animals (Chi^2 Test). These results indicate that other factors may account for the significant differences in fighting behavior of group-reared animals in home and other-home cages compared with neutral ones.

The data for the other behavioral items affected by cage but not by sequence are given in Table 5. These include digging, investigating the genitalia, grooming the genitalia, and boxing.

The frequency of digging varied significantly with location of the match for group-reared males (Friedman, $p < .01$), group-reared females (Friedman, $p < .05$), and for individually-reared males (Friedman, $p < .05$). For all three groups digging was significantly more frequent in other-home than in home cages (Sign test, grouped males, $p < .01$; grouped females, $p < .05$; individually-reared males, $p < .02$), while there were no significant differences in digging behavior between home and neutral cages or between other-home and neutral cages.

The effects of the cage were significant for group-reared males and females for investigating the genitalia (Friedman, $p < .01$ for males; $p < .05$ for females). For group-reared males the frequency of the behavior was greater in neutral than in other-home cages (Sign test, $p < .001$). For group-reared females there was no significant difference between any two situations.

Table 3. Record of which animal is first to attack in home (other) observational cage and in neutral cage (for mutual attacks only)

	Group-reared males N = 20	Group-reared females N = 24	Individually-reared males N = 10	Individually-reared females N = 18
No. of matches in which resident animal attacks first	1	7(5)*	2	6
No. of matches in which introduced animal attacks first	1	3(1)*	2	3
No. of matches in which first attack is mutual in home (other) cage	5	3	1	8
No. of matches in which first attack is mutual in neutral cage	no fights	0	1	1

*Two of the seven resident animals were also the first to attack when they were introduced. The Chi^2 analysis therefore was made with the frequencies indicated in parentheses.

Table 4. Record of wins and losses in home (other) observational cage and in neutral cage (for mutual attacks only)

	Group-reared males N = 20	Group-reared females N = 24	Individually-reared males N = 10	Individually-reared females N = 18
No. of matches in which resident won	4(3)*	6(3)*	1	7(2)*
No. of matches in which introduced animal won	2(1)*	6(3)*	3	7(2)*
No. of matches in which neither animal won in home (other) cages	1	1	1	3
No. of matches in which neither animal won in neutral cages	no fights	0	0	0

*Numbers in parentheses represent these on which the Chi^2 analysis was based. The other animals were those which won when residents and when introduced.

Table 5. Medians and ranges for behavior patterns in which cage, but not sequence, had significant effects

		Group-reared		Individually-reared	
Behavior pattern	Cage	Males N = 20	Females N = 24	Males N = 10	Females N = 18
Investigating genitalia	Home	3 0 - 13	2.0 0 - 20	0 0 - 14	0 0 - 5
	Other	2 0 - 8	2.0 0 - 21	0 0 - 6	0 0 - 1
	Neutral	5.5 0 - 16	7.0 0 - 18	0.5 0 - 13	0 0 - 2
Grooming genitalia	Home	7.0 0 - 34	10.0 0 - 32	0 0 - 8	0 0 - 7
	Other	6.0 1 - 22	8.0 0 - 37	0 0 - 9	0 0 - 1
	Neutral	6.5 0 - 53	6.5 1 - 37	0.5 0 - 3	0 0
Boxing	Home	0 0 - 1	0 0 - 19	0 0 - 1	3.5 0 - 34
	Other	0 0 - 1	0 0 - 19	0 0 - 3	3.5 0 - 34
	Neutral	0 0 - 2	0 0 - 13	1.0 0 - 3	15.0 1 - 58
Digging	Home	23.5 0 - 90	23.5 0 - 64	6.0 0 - 25	0 0 - 20
	Other	46 4 - 106	46.5 1 - 83	15.5 0 - 42	3.5 0 - 31
	Neutral	28.5 1 - 67	29.0 3 - 60	7.0 0 - 33	1.0 0 - 10

Other behavior patterns which were affected by the location of the match only were grooming the genitalia in group-reared females (Friedman, $p < .05$) in which the frequency was higher in home than in neutral cages (Sign test, $p < .01$) and boxing in individually-reared females (Friedman, $p < .02$) in which the frequency in neutral cages exceeded that in other-home cages (Sign test, $p < .02$).

2) Inter-group cage effects

The above intra-group effects of the observational cage were taken into account in that all group comparisons were made within each cage situation by means of the Kruskal-Wallis one-way analysis of variance (Siegel, 1956). For the behavior patterns in which only the cage had a significant effect on their frequency, the following group differences were found to be significant:

a) Fighting behavior (see Table 2)

The frequency of fighting differed among the four experimental groups in home cages ($p < .01$), in other-home cages ($p < .001$) and in neutral cages ($p < .001$). In home cages the significant differences appeared between individually-reared males and females in which the latter showed a higher frequency ($p < .01$), and between individually-reared and grouped females in which the former fought more ($p < .01$). In other-home cages also, the significant differences were between individually-reared males and females ($p < .01$), and between individually-reared and grouped females ($p < .01$). The direction of the differences were the same. In neutral cages, these same two pairs of groups showed the same significant differences (individually-reared females > individually-reared males, $p < .01$; individually-reared females > grouped females, $p < .001$), and individually-reared males also fought more frequently than grouped males ($p < .01$).

The frequency of attack differed among the groups in home ($p < .02$) and in neutral cages ($p < .01$). In the home cage individually-reared females attacked each other more than individually-reared males ($p < .01$) and more than group-reared females ($p < .02$). In neutral cages individually-reared females also exceeded grouped females ($p < .01$) in this behavior.

The four groups also differed significantly in the amount of time spent in fighting in all three cage situations ($p < .001$). In home and other-home cages individually-reared females again exceeded individually-reared males ($p < .001$ in home; $p < .01$ in other-home) and grouped females ($p < .001$ for both). In neutral cages individually-reared females spent more time fighting than group-reared females ($p < .001$), and individually-reared males fought more than grouped males ($p < .01$).

Fight latency differed among groups in home ($p < .01$), other-home ($p < .01$) and neutral ($p < .001$) cages. Comparisons between pairs of groups showed that individually-reared females had a lower fight latency than grouped females in home ($p < .05$), other ($p < .05$) and neutral ($p < .001$) cages and lower than individually-reared males in home ($p < .01$) and other-home ($p < .01$) cages. Individually-reared males also had a shorter fight latency than group-reared males ($p < .01$) in neutral cages.

b) **Non-fighting behavior patterns**

Table 5 shows the other four behavior patterns in which cage but not sequence significantly influenced their frequency. For investigating the genitalia, grooming the genitalia, boxing, and digging there were significant differences in all three cages among the four experimental groups ($p < .01$ for boxing in home and other-home cages; $p < .001$ for all other).

For investigating the genitalia there were no significant sex differences, but group-reared males exceeded individually-reared males in home ($p < .05$) and in neutral ($p < .02$) cages, and grouped females did this more frequently than individually-reared females in home ($p < .01$), other-home ($p < .001$), and neutral ($p < .001$) cages. Grooming the genitalia showed the same trend with group-reared males surpassing individually-reared ones in home ($p < .01$), other-home ($p < .001$) and neutral ($p < .01$) cages, and grouped females exceeding individually-reared ones in all three cages ($p < .001$) as well.

Individually-reared females boxed more frequently than individually-reared males and grouped females in home and other-home cages ($p < .01$ for all cases) and in neutral cages ($p < .001$ in both cases). Individually-reared males boxed more than grouped males in neutral cages only ($p = .05$).

c. Effects of both observational sequence and observational cage on behavior

The three behavior patterns affected by both the sequence of matches and the observational cage are shown in Table 6. These include nosing, investigating the chin, and investigating the mid-ventral gland. In no case was both cage and sequence significant within the same group so that intra-group effects of cage and sequence were analyzed separately.

Table 6. Medians and ranges for behavior patterns affected by cage and sequence

			Group-reared		Individually-reared	
Behavior pattern	Cage	Match #	Males N = 20	Females N = 24	Males N = 10	Females N = 18
Nosing	Home	1	9.5 5 - 12	8 6 - 13	27 17 - 37	29 27 - 45
		2	2.5 1 - 9	6.5 2 - 20	34 20 - 37	26 11 - 34
		3	7.5 0 - 53	6.5 2 - 15	26 11 - 34	13 6 - 35
	Other	1	11 0 - 17	7.5 5 - 13	22 21 - 23	38 23 - 56
		2	7.5 1 - 10	6 4 - 16	23 16 - 28	33 23 - 36
		3	7 1 - 16	9 1 - 16	18 11 - 26	15 4 - 36
	Neutral	1	18 7 - 26	11.5 7 - 24	24 4 - 37	16.5 8 - 59
		2	13.5 9 - 23	12.5 5 - 27	20 13 - 31	19.5 4 - 41
Investigating the chin	Home	1	2 1 - 11	5 1 - 8	1 1 - 1	3 2 - 6
		2	1 0 - 2	2 0 - 5	1 0 - 5	0 0 - 4
		3	0.5 0 - 6	1 0 - 4	2 1 - 6	0 0 - 5
	Other	1	3 1 - 13	1.5 0 - 8	6.5 6 - 7	4 0 - 7
		2	3.5 2 - 6	2 1 - 6	2 0 - 13	3 1 - 4
		3	0.5 0 - 3	1 0 - 3	1 1 - 4	0 0 - 1
	Neutral	1	3.5 1 - 11	3 0 - 7	1 0 - 12	1 0 - 7
		2	4.5 1 - 13	3 2 - 9	2.5 1 - 5	1 0 - 8

continued on next page

Table 6. (continued)

Investigating the midventral gland	Home	1	2.5 2 - 5	3.5 3 - 6	0.5 0 - 1	1 0 - 8
		2	3 1 - 8	0.5 0 - 10	0 0 - 0	0 0 - 0
		3	1 0 - 4	1 0 - 7	0 0 - 2	0 0 - 1
	Other	1	1 0 - 5	1 0 - 4	2 1 - 3	1 0 - 2
		2	2 1 - 6	1 1 - 3	1 0 - 1	0 0 - 0
		3	0.5 0 - 3	0.5 0 - 3	0 0 - 2	0 0 - 0
	Neutral	1	5 1 - 19	3 0 - 14	1 0 - 4	0.5 0 - 1
		2	6.5 0 - 18	2.5 0 - 11	1 1 - 3	0 0 - 3

1) Intra-group effects of cage and sequence

Nosing: sequence of matches was statistically significant for individually-reared females only (Friedman, $p < .05$). The frequency of nosing decreased between matches one and three (Sign test, $p < .01$) for this group. The frequency of nosing differed with cage for group-reared males (Friedman, $p < .001$) and group-reared females (Friedman, $p < .01$). For both groups nosing was significantly more frequent in neutral than in home (Sign test, $p < .01$ for males; $p < .02$ for females) or in other-home (Sign test, $p < .01$ for males; $p < .05$ for females) cages.

Investigating the chin: sequence of matches was statistically significant for individually-reared (Friedman, $p < .02$) and group-reared female (Friedman, $p < .001$). The frequency of chin investigations decreased between matches one and three for the first group (Sign test, $p < .01$) and decreased between matches two and three for the second group (Sign test, $p < .001$). The cage had a significant effect on this behavior pattern in group-reared males (Friedman, $p < .05$) in which the frequency was greater in neutral than in home cages (Sign test, $p < .05$).

Investigating the midventral gland: sequence of matches was statistically significant for individually-reared females only (Friedman, $p < .05$). The frequency of this behavior decreased between matches one and two (Sign test, $p < .01$) and between matches one and three (Sign test, $p < .01$). The effect of the cage was significant for this behavior in group-reared males and females (Friedman, $p < .001$ for males; $p < .02$ for females). For group-reared males the frequency was greater in neutral than it was in home (Sign test, $p < .01$) or in other-home (Sign test, $p < .01$) cages. For group-reared females the frequency was greater in neutral than in other-home cages (Sign test, $p < .02$).

2) Inter-group comparisons of behavior patterns affected by both cage and sequence

Table 6 shows the medians and ranges of scores for the four groups for the three behavior patterns in which both cage and sequence affected the frequency. Group comparisons were made between equivalent situations only (i.e., within both cage and sequence) by means of the Kruskal-Wallis one-way analysis of variance (Siegel, 1956).

Nosing differed significantly among the groups in home and other-home cages in all three matches ($p < .01$) but not in neutral cages in any match. In home cages individually-reared males nosed more than grouped males in all three matches ($p < .05$, $p < .05$, $p < .02$ respectively). In other-home cages individually-reared males also nosed more in all three matches ($p < .05$, $p < .05$, $p < .02$ respectively); and individually-reared females nosed more than grouped females in matches one ($p < .01$) and two ($p < .02$).

The frequency of investigating the chin showed significant group differences only in other-home cages in match three ($p < .05$) in which individually-reared males did this more than individually-reared females ($p < .01$), and in neutral cages in match two ($p < .05$) in which group-reared females did it more than individually-reared females ($p < .01$).

Investigating the midventral gland showed significant variations in home cages in the second match ($p < .05$), in other-home cages in the second match ($p < .02$), and in neutral cages in both the first ($p < .01$) and second ($p < .001$) matches. Grouped females investigated their partner's midventral gland more than individually-reared females in other-home cages in match two ($p < .02$), and in neutral cages in matches one ($p = .02$) and two ($p < .01$). Grouped males exceeded individually-reared males in this behavior pattern in home cages in match two ($p < .05$) and in neutral cages in matches one ($p < .02$) and two ($p < .05$). They also exceeded grouped females in home cages in match two ($p < .05$). Individually-reared males did this more than individually-reared females in neutral cages in match two ($p < .05$).

d. Behavior patterns showing no effects of observational sequence or cage type

The behavior patterns listed in Table 7 showed no significant differences within any group with either the observational sequence or the cage in which the match occurred. These include mounting, grooming, grooming the chin, grooming the midventral gland, self-grooming, self-grooming the genitalia, skimming, defense, hipping, and foot-stomping.

Of these, the following differed significantly among the four experimental groups (Kruskal-Wallis one-way analysis of variance, Siegel, 1956): grooming ($p < .001$), grooming the chin ($p < .001$), grooming the genitalia ($p < .001$), defense ($p < .01$), hipping ($p < .05$), and self-grooming ($p < .01$). The significant differences were found for these behavior patterns between the following pairs of groups (Kruskal-Wallis one-way analysis of variance):

Table 7. Medians and ranges for behavior patterns in which neither cage nor sequence had significant effects

	Group-reared		Individually-reared	
Behavior pattern	Males N = 20	Females N = 24	Males N = 10	Females N = 18
Mounting	0 0 - 20	0 0 - 5	0 0 - 2	0 0
Grooming	9 1 - 31	10 0 - 33	10 0 - 35	1.5 0 - 26
Grooming the chin	1 0 - 7	0 0 - 12	2 0 - 10	0 0 - 4
Grooming the midventral gland	1 0 - 7	1 0 - 9	0 0 - 2	0 0 - 3
Self-grooming	6 0 - 29	7 0 - 56	4.5 0 - 11	10 0 - 78
Self-grooming genitalia	0 0 - 7	0 0 - 4	0 0 - 3	0 0 - 2
Skimming	0 0 - 23	0 0 - 2	0 0 - 11	0 0 - 9
Defense	0 0 - 63	0 0 - 37	0 0 - 68	0.5 0 - 87
Hipping	0 0 - 27	0 0 - 50	0 0 - 36	0 0 - 37
Foot-stomping	0 0 - 24	0 0 - 19	0 0 - 13	0 0 - 7

<u>Group-reared males vs. group-reared females</u>: no significant differences were found in any of these behavior patterns.

<u>Individually-reared males vs. individually-reared females</u>: males exceeded females in the frequency of grooming ($p < .001$) and grooming the chin ($p < .001$), while females surpassed males in the frequency of self-grooming ($p < .01$).

<u>Group-reared females vs. individually-reared females</u>: individually-reared females showed a higher frequency of defensive behavior ($p < .01$) and self-grooming ($p < .05$), while group-reared females groomed ($p < .001$), groomed the chin ($p < .01$) and the midventral gland ($p < .001$) more than individually-reared females.

<u>Group-reared males vs. individually-reared males</u>: individually-reared males groomed the chin more frequently ($p < .05$), and group-reared males groomed the midventral gland more frequently ($p < .001$).

3. Correlations between attacking and other behavior patterns

A Spearman Rank Correlation Coefficient (rho), corrected for tied observations (Siegel, 1956), was calculated between the frequency of attacking, since this was considered the best measure of individual aggressiveness, and all other non-fighting behavior patterns not affected by observational sequence for each group in each of the three different observational situations.

For group-reared males, attacking was significantly correlated with hipping in home (rho = .74, $p < .01$) and in other-home (rho = .73, $p < .01$) cages. Defensive behavior (rho = .52, $p < .05$) and investigating the genitalia (rho = .46, $p < .05$) were also found to be significantly correlated with attacking in other-home cages.

Group-reared females also showed a significant correlation between attacking and hipping in home (rho = .58, $p < .01$) and other-home cages (rho = .85, $p < .01$). The following behavior patterns were also correlated with frequency of attack, but only in other-home cages: investigating the genitalia (rho = .44, $p < .05$), foot-stomping (rho = .39, $p < .05$), boxing (rho = .51, $p < .01$), mounting (rho = .38, $p < .05$), and grooming the genitalia (rho = .36, $p < .05$).

Behavioral correlations for individually-reared males were significant between attacking and boxing in home cages (rho = .86, $p < .01$), hipping in home (rho = .71, $p < .05$) and in other-home cages (rho = .81, $p < .01$) and in neutral cages (rho = .92, $p < .01$), and mounting in neutral cages (rho = .66, $p < .05$). Significant negative correlations were found between attacking and grooming the other animal (rho = -.62, $p < .05$).

For individually-reared females the behavior patterns which showed significant correlations with attacking were hipping in home (rho = .67, $p < .01$), other (rho = .39, $p = .05$), and neutral (rho = .74, $p < .01$) cages, self-grooming in other-home cages (rho = .39, $p = .05$), digging in other-home cages (rho = .56, $p < .05$), and boxing in home cages (rho = .43, $p < .05$). Defense was negatively correlated with attacking in home (rho = -.59, $p < .01$) and in other-home (rho = -.79. $p < .01$) cages.

4. Effects of other variables in fighting behavior

It is possible that other variables such as time of day, relative humidity, temperature, season, and weight of the animals might affect the tendency to fight. Since the temperature was controlled and all matches occurred during one season, these factors can be considered constants. Table 8 shows the distribution of matches in which fights occurred for all groups among one-hour time intervals. Fighting is entirely random with respect to the time periods under consideration (Chi^2 $p = 0.9$). It should be noted that matches for each of the four groups of gerbils were distributed as evenly as possible with respect to time. From Table 9 it can be seen that there are a proportionally greater number of matches with fights below 60% relative humidity than above, but this does not reach the level of statistical significance.

With regard to weight, it might be hypothesized that, while this should not affect the tendency to fight, it might determine the outcome of a fight. In the fifty matches in which it was possible to determine which animal(s) was last to attack (i.e., was the winner), the heavier participant was victorious in twenty-two, while the lighter won twenty-eight matches (Chi^2 $p < 0.9$ based on eighteen and seventeen respectively, correcting for individuals that won more than once). Hence, under the conditions of this experiment, relative weight is unimportant in determining the outcome of a fight.

A factor which was important in the determination of fight outcome, however, was which animal was the first to attack. In fifty-six cases the first animal to attack was also the last to attack and was therefore considered to have won it; the first to attack lost the match in twenty instances (Chi^2 $p < .001$ based on thirty and eight respectively, correcting for individuals counted more than once).

While the techniques of this study were not refined enough to permit direct analysis of the possible effects of the estrus cycle, there was no evidence to suggest that female fighting was cyclical

Table 8. Incidence of all animals fighting during one-hour time intervals

Time	9-10 AM	10-11 AM	11-12 AM	12-1 PM	1-2 PM	2-3 PM	3-4 PM
Matches with fighting	0	7	14	16	10	7	2
Matches without fighting	1	10	15	15	11	5	1

x^2 $p=0.9$

Table 9. Incidence of all animals fighting during 10% relative humidity intervals

Relative humidity	40-49%	50-59%	60-69%	70-79%	80-89%
Matches with fighting	8	20	19	8	1
Matches without fighting	4	13	29	10	2

x^2 $p > 0.1$

in nature.

5. Pattern of results for individual animals

The pattern of results for individual animals involved in a sequence of three matches appears in Table 10. An animal was scored as a winner (W) even if the match ended in a mutual attack so that it was possible for both animals to be scored as winners in the same match. A Chi^2 test shows that the distribution of result patterns is not random ($p < .001$). The patterns which occur much more than would be expected by chance are those which are consistent between two or more consecutive matches (NNN, NNL, NWW, WWW). Those patterns which do not appear at all are those in which the results are different between matches one and two and between matches two and three (WLW, NWN, LWN, WNL, LNL, LWL). This shows a general consistency of individuals between consecutive matches, particularly for non-fighters, most of which are group-reared gerbils.

Table 10. Pattern of sequential results for individual animals

Sequential results	Group-reared Males N = 20	Group-reared Females N = 24	Individually-reared Males N = 10	Individually-reared Females N = 18	Total N = 72
WWW		1		4	5
WWL				2	2
WLL			1	2	3
WLW					0
LLL				2	2
LLW			1	2	3
LWW				2	2
LWL					0
NNN	10	5	2		17
NNW	2	1			3
NNL	1	7			8
NWN			1		1
NLN		1	1		2
WNN	3				3
LNN	1				1
NLL	1	2			3
LNL					0
LLN				1	1
NWW	1	5	1		7
WNW					0
WWN			1	1	2
NLW		1		1	2
NWL	1			1	2
LWN					0
WLN			1		1
WNL					0
LNW		1	1		2

N = no fight

W = win

L = loss

Population Dynamics

Figures 2 and 3 show the changes in numbers of gerbils for two confined populations, designated "high density" and "low density" respectively. These names are maintained throughout despite their later inappropriateness.

1. Population changes, survival, and birth records

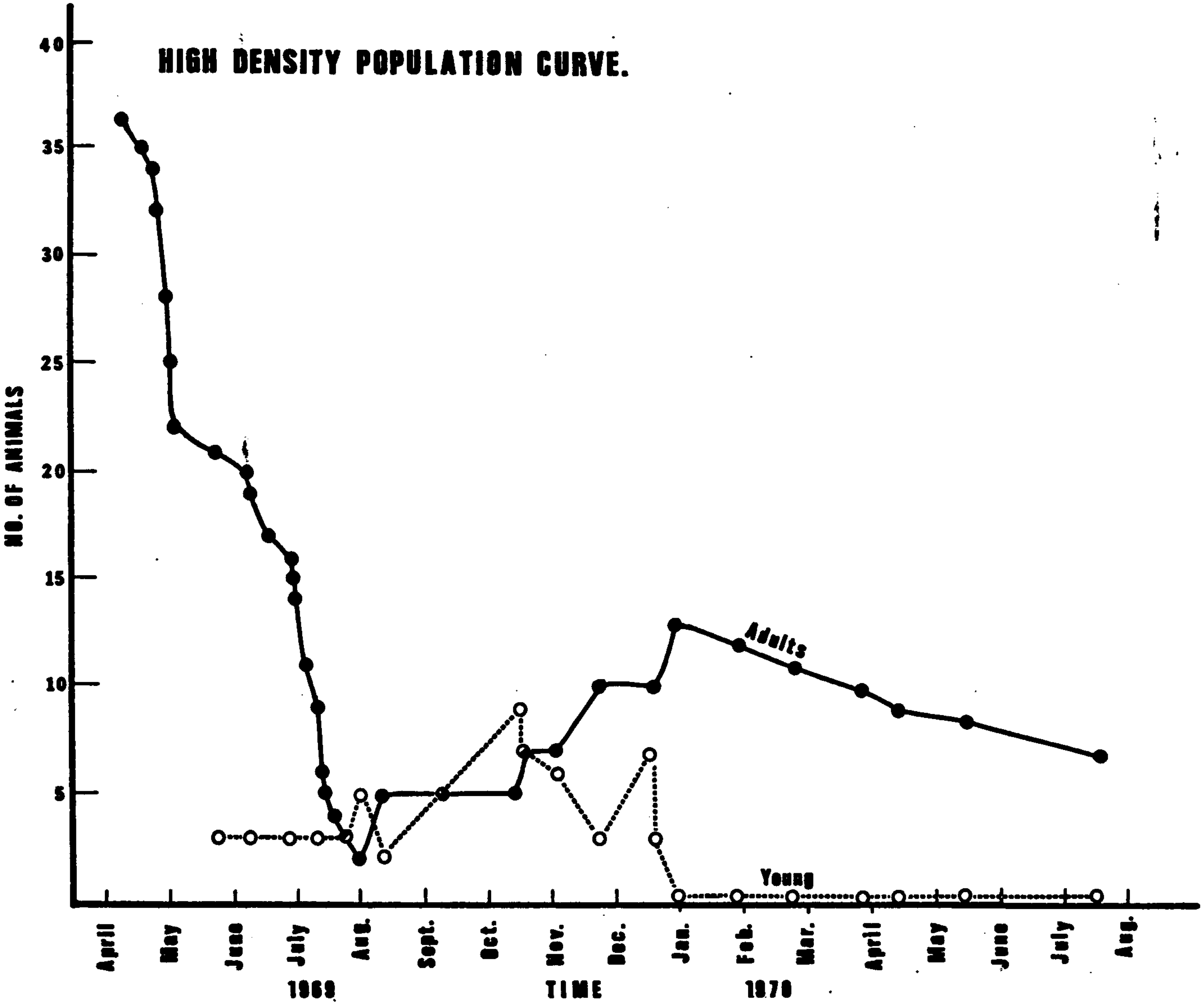
a. High density population

The high density population was begun by releasing thirty-six adult gerbils on April 9, 1969. There followed a period of almost four months of intense fighting in which there was a sharp drop in the number of gerbils so that by July 29, 1969 there remained only two of the original animals, one male and one female. The first seventeen animals which died were males while the remaining seventeen were females. All of these were extensively wounded.

From a low of two adults, the population increased slowly for about five months until it reached a peak of thirteen, four males and nine females. About one month later, the dominant male remaining from the founding population began to attack a female from the third successful litter, eventually causing her death. This new upsurge of fighting began after six months without any fighting. Two more females and two males were subsequently attacked and killed, and one female died from natural causes, reducing the population to seven animals at the end of fifteen months and six days. At the termination of this study, after sixteen months, two of the remaining seven animals were under attack.

The broken line in Figure 2 represents the number of young surviving twenty-four hours or more. They were assumed to have reached

Figure 2. Graph showing changes in population size in the high density population. Number of adults is shown in solid lines and number of young surviving 24-hours in dashes.


HIGH DENSITY POPULATION CURVE.
NO. OF ANIMALS
40
35
30
25
20
15
10
5
Adults
Young
April
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
April
May
June
July
Aug.
1969
TIME
1970

adulthood at eleven weeks of age, since gerbils reportedly mature sexually between ten and twelve weeks (Schwentker, 1963). Table 11 shows the birth and survival record in the high density population and relates this to the number of animals present at parturition. The number born represents the pups found, alive or dead, and probably is somewhat less than the actual number born since some may have been completely cannibalized or buried in the substrate and, therefore, overlooked. During the period of intense fighting which occurred during the first few months, litter survival was extremely poor. Pups were either ignored at birth or cannibalized. The first four litters had been conceived prior to the beginning of the experiment. Only one female successfully bred and reared young during the course of sixteen months, even though there were several mature females with opportunity to do so.

When the density of the population was reduced, litter survival improved considerably, and a total of eleven young survived to sexual maturity. However, none of the pups in the last two litters survived. At the time of their birth the adult population had risen to ten. No litters were born during the eight-month period when the adult population rose to thirteen and was subsequently reduced to seven.

b. Low density populations

The first low density population was begun on April 9, 1969 by releasing two adult males and two adult females into the other fifty square foot enclosure. There followed several days of fighting which ended on the sixth day with the death of one of the males. For the remainder of the time, the survivors coexisted without conflict. However, since none of the pups from the five litters that were born

Table 11. Birth and survival record of litters born in the high density population and number of animals in the population at the time of birth

Date of birth	No. in litter	Mother no.	No. surviving to weaning	% surviving to weaning	No. of adults	No. of young
4/14/69	3	unknown	0	0	36	0
4/17/69	3	unknown	0	0	36	0
4/18/69	6	unknown	0	0	36	0
5/2/69	5	unknown	0	0	22	0
5/21/69	6	3	3	50.0%	22	0
8/1/69	3	3	2	66.6%	2	3
9/8/69	3	3	3	100.0%	5	2
10/13/69	5	3	3	60.0%	5	5
11/23/69	2	3	0	0	10	0
12/17/69	4	unknown	0	0	10	7

survived (most were cannibalized), these gerbils were removed on July 18, 1969. It was decided to repeat the experiment with different individuals.

Accordingly, a second low density population was begun by releasing two males and two females into the enclosure. This time the gerbils selected had been caged together prior to their release so that initially no fighting occurred. The growth curve for this population is shown in Figure 3. The adult population rose to eight by the middle of October. About a month later, fighting began for the first time, and one of the original females died a few days later. This outbreak of fighting occurred one month after the sexual maturation of the first litter. Fighting again began on March 24, 1970, about two weeks after the maturation of the young from the second litter when the number of adults had again reached eight. It continued with one animal after another becoming the victim of attack until the number of adults dropped to three after ten and a half months. Fighting then ceased for the remainder of the twelve-and-a-half month study.

The record of births and survival for this population is presented in Table 12. Survival for the first litter was good, while there were four adults living together harmoniously. As the number of adults increased after the maturation of this first litter, litter survival was adversely affected. When the number of adults was later reduced as a result of fighting, litter survival increased considerably; in the last two litters born during the study, 100% and 75% survived to weaning when there were three and four adults present, respectively. As in the high density population, not all mature

Figure 3. Graph showing changes in population size in the low density population. Number of adults is shown in solid lines and number of young surviving 24-hours in dashes.

LOW DENSITY POPULATION CURVE

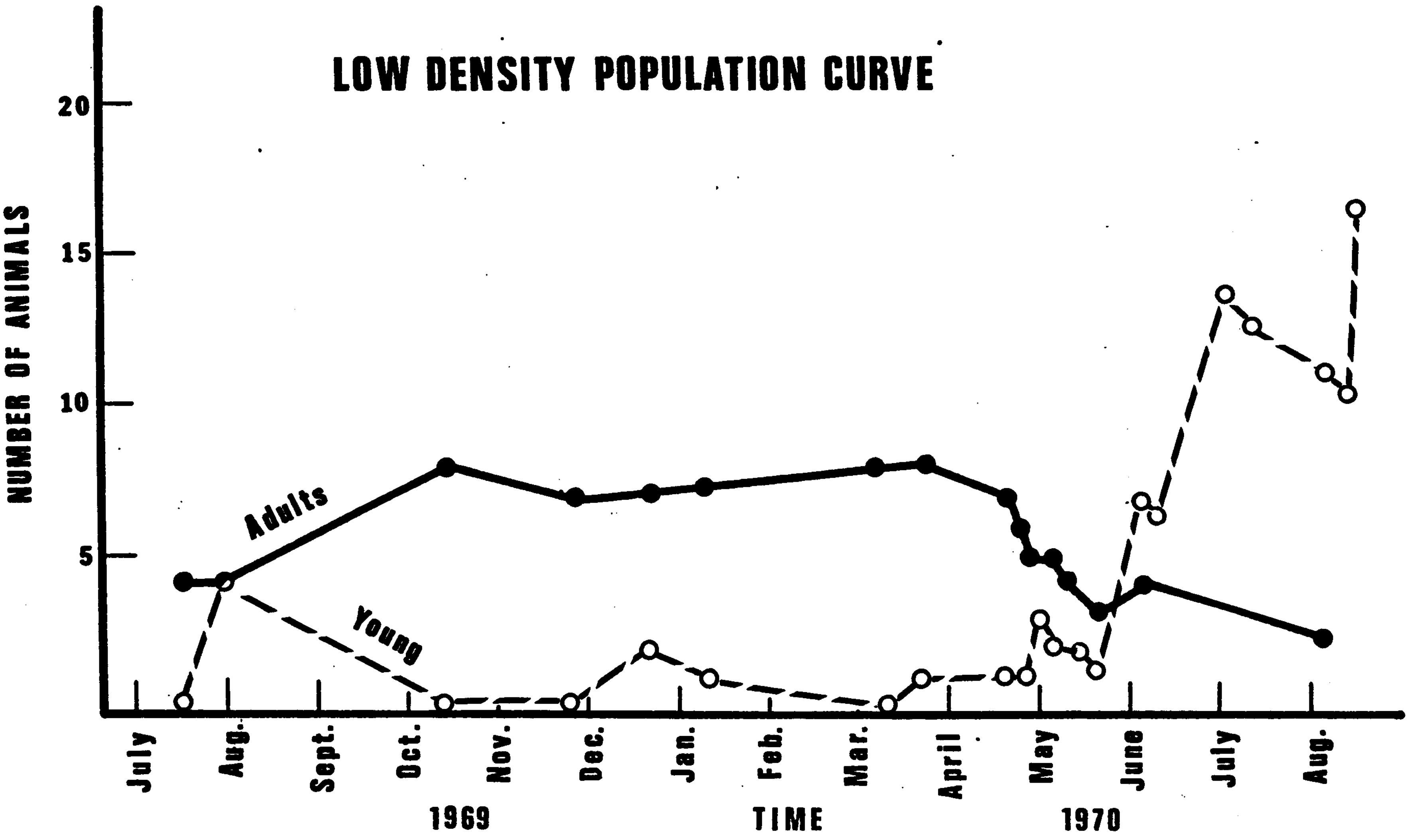


Table 12. Birth and survival record of litters born in the low density population and number of animals in the population at the time of birth

Date of birth	No. in litter	Mother no.	No. surviving to weaning	% surviving to weaning	No. of adults present	No. of young present
7/31/69	4	2	4	100.0%	4	0
12/21/69	2	4	1	50.0%	7	0
1/28/70	1	4	0	0	7	1
3/22/70	4	4	1	25.0%	8	0
4/30/70	2	6	0	0	6	1
5/10/70	4	4	0	0	5	2
6/6/70	6	6	6	100.0%	3	1
7/7/70	8	6	6	75.0%	4	6
8/7/70	6	6	5	83.3%	3	11

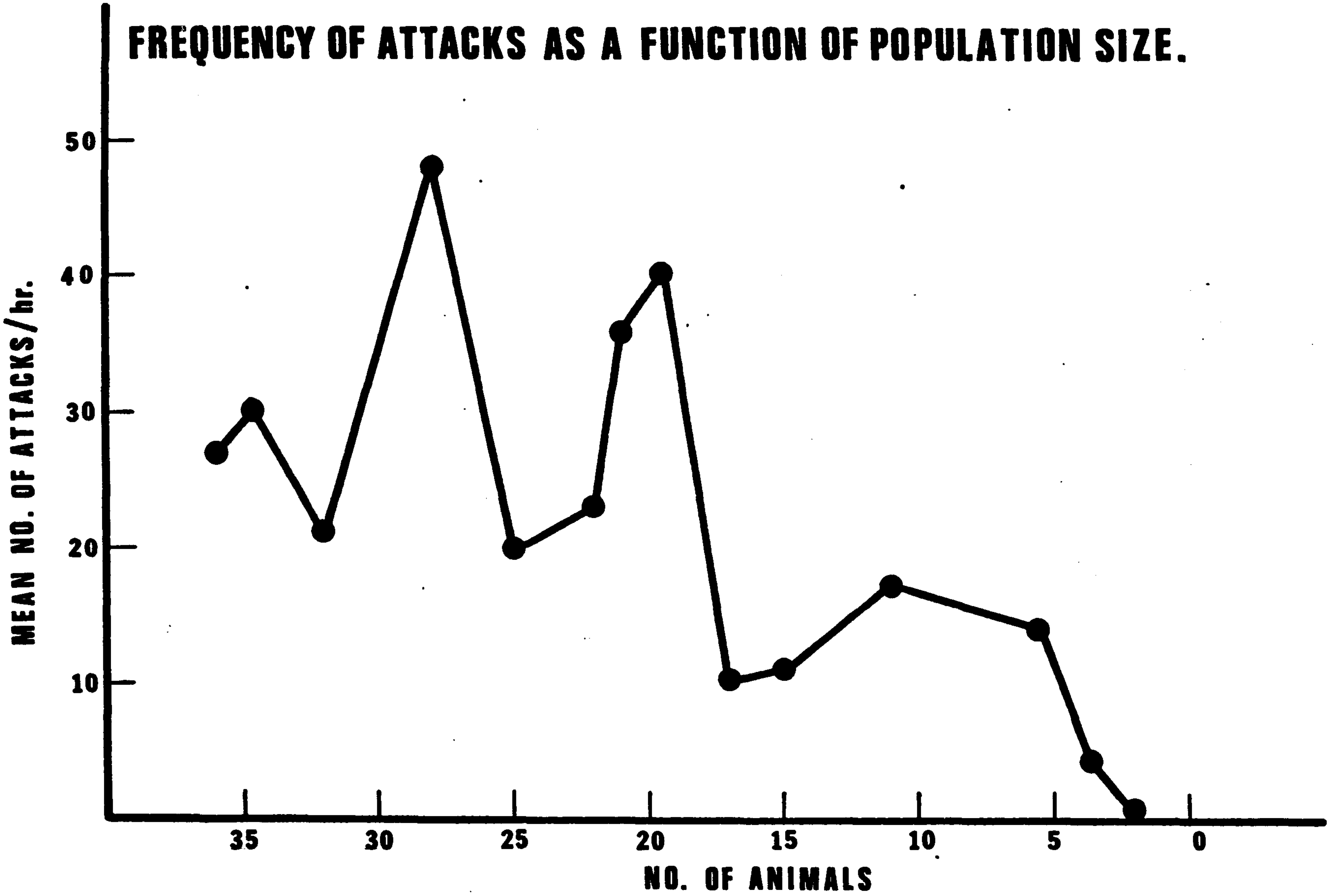
females were actively reproducing.

2. Frequency of fighting in relation to density

If fighting behavior is related to population density, it might be expected that the frequency or rate of fighting would be proportional to the number of animals interacting in the enclosure. Figure 4 shows the changes in frequency of aggressive interactions (i.e., fights, attacks, and chases), which occurred during the initial decline in the high density population. Although it fluctuated considerably, the mean number of attacks per hour remained uniformly high until the number of animals in the population fell to about four. This graph represents total attacks and total number of animals without regard to sex.

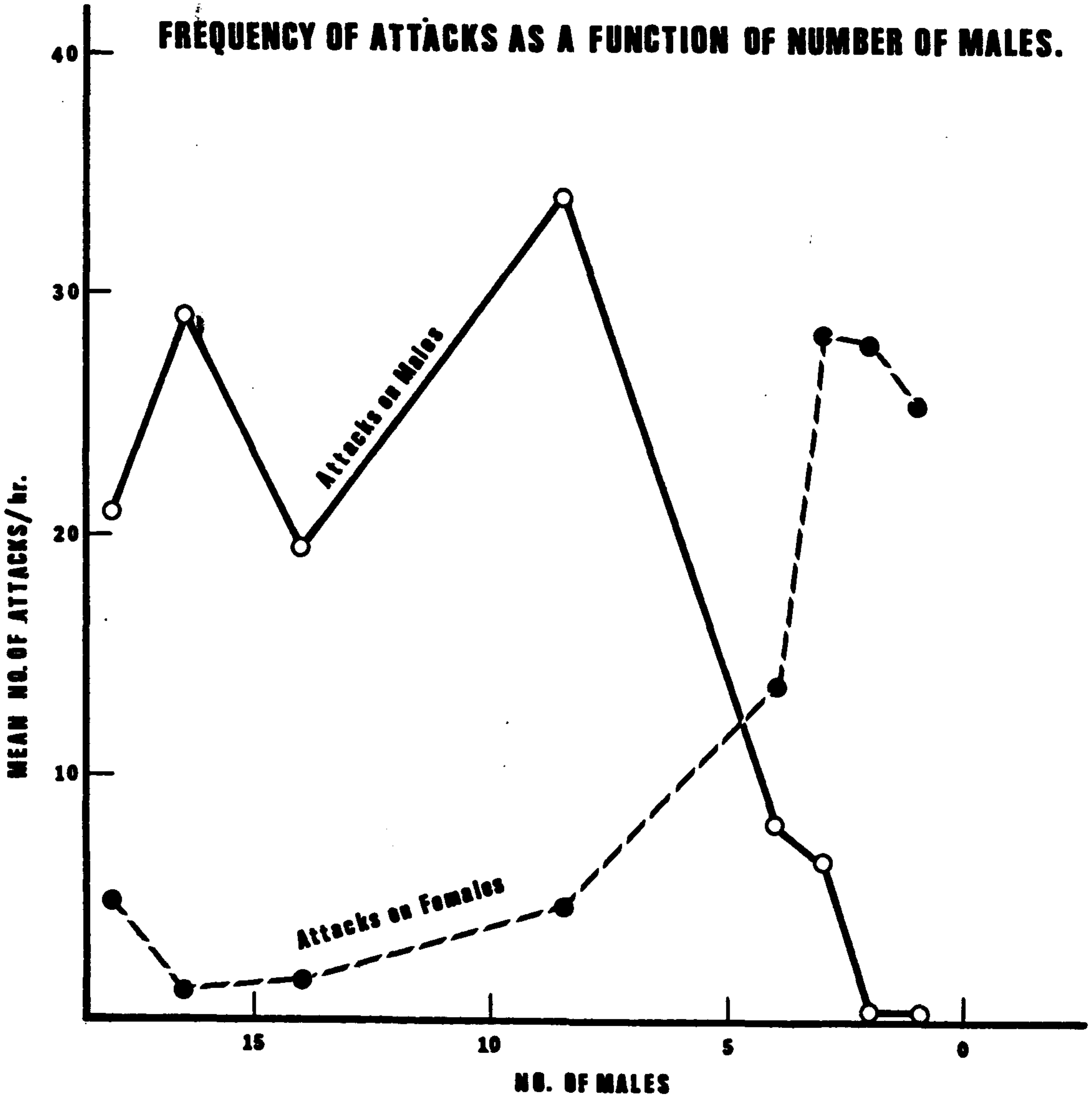
Figure 5 indicates the changes in frequency of attacks on males and on females with the declining number of males in the population. As the number of males drops below eight, there is a correspondingly sharp reduction in the frequency of attacks on males. At the same time, the initially low frequency of attacks on females makes a sharp increase. Figure 6 indicates that during the time when more than one male was present, the frequency of attacks on females was moderate. It rose sharply, however, as the males were eliminated, and then began to decline sharply as the number of females decreased. Thus, while the frequency of attack is not proportional to the total density, the sex-specific frequency is roughly proportional to the number of animals of each sex present at a given time.

Figure 4. Frequency of attacks in relation to population density.



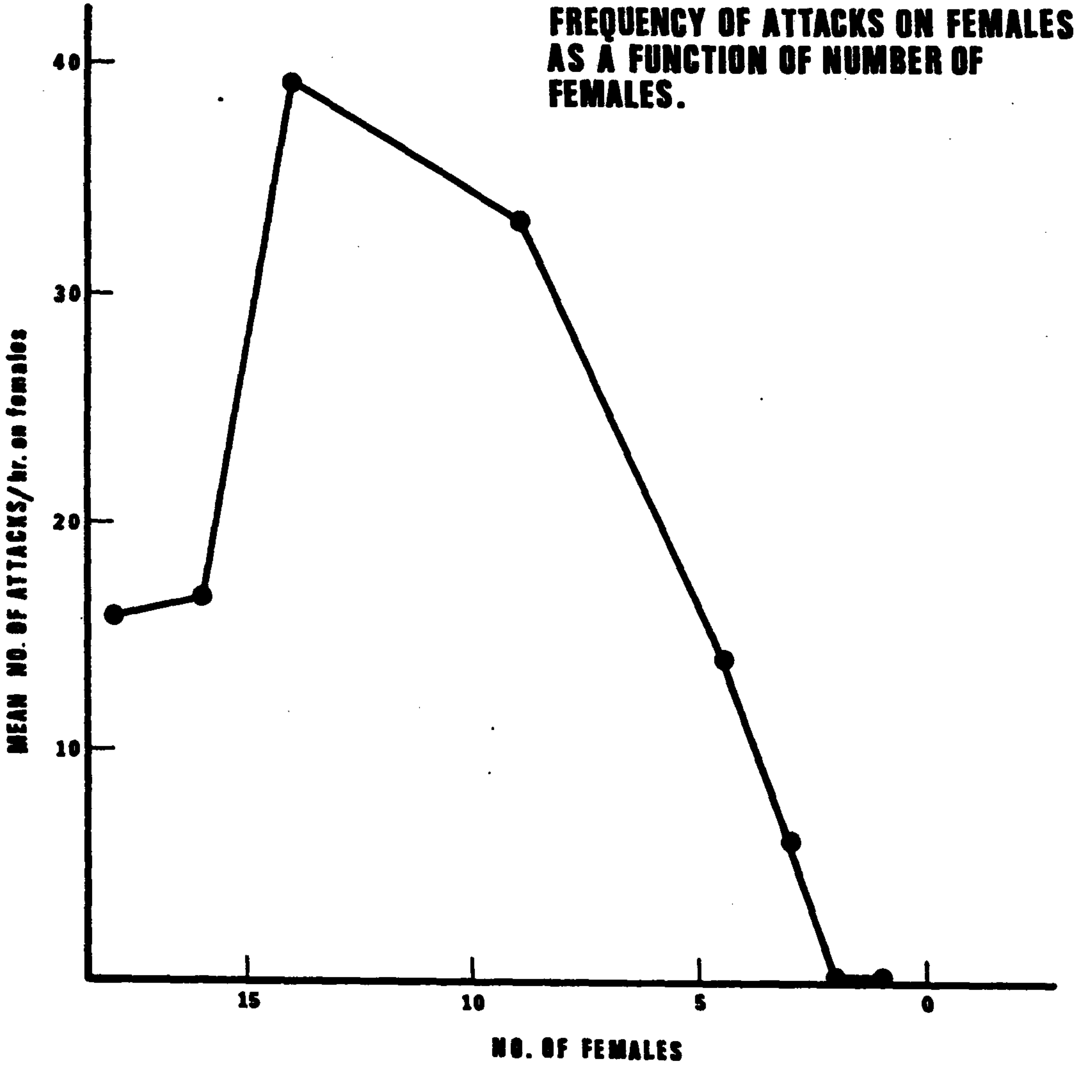
FREQUENCY OF ATTACKS AS A FUNCTION OF POPULATION SIZE.

Figure 5. Frequency of attacks on males (solid lines) and on females (dashes) in relation to the number of males present in the population.



FREQUENCY OF ATTACKS AS A FUNCTION OF NUMBER OF MALES.

Figure 6. Frequency of attacks on females in relation to the number of females present in the population.



FREQUENCY OF ATTACKS ON FEMALES AS A FUNCTION OF NUMBER OF FEMALES.

3. Other variables affecting fighting behavior

It is possible that variables other than density might affect the frequency of aggressive interactions. The three variables analyzed for their possible influence were temperature, relative humidity, and time of day. Table 13 presents the mean number of attacks per hour for successive temperature intervals. The frequency of attack increases significantly between the three successive temperature intervals ($p < .05$, Mann-Whitney U Test).

From Figure 7 it can be seen that the number of attacks per hour is slightly, but not significantly higher at relative humidities between 40% and 59% than below 40%. At humidities above 59%, however, there is a statistically significant ($p < .05$, Mann-Whitney U Test) drop in the frequency of aggressive encounters.

4. Social organization

During the first two days after release, most of the animals in the high density population were observed to have at least one aggressive interaction with another animal. These early encounters were characterized by mutual fighting between pairs of gerbils. By the third day of observation, and at all times thereafter, there was a complete absence of mutual fighting, and aggressive interactions were entirely uni-directional. At the same time, a total of eight animals, four males and four females were responsible for all the observed attacks.

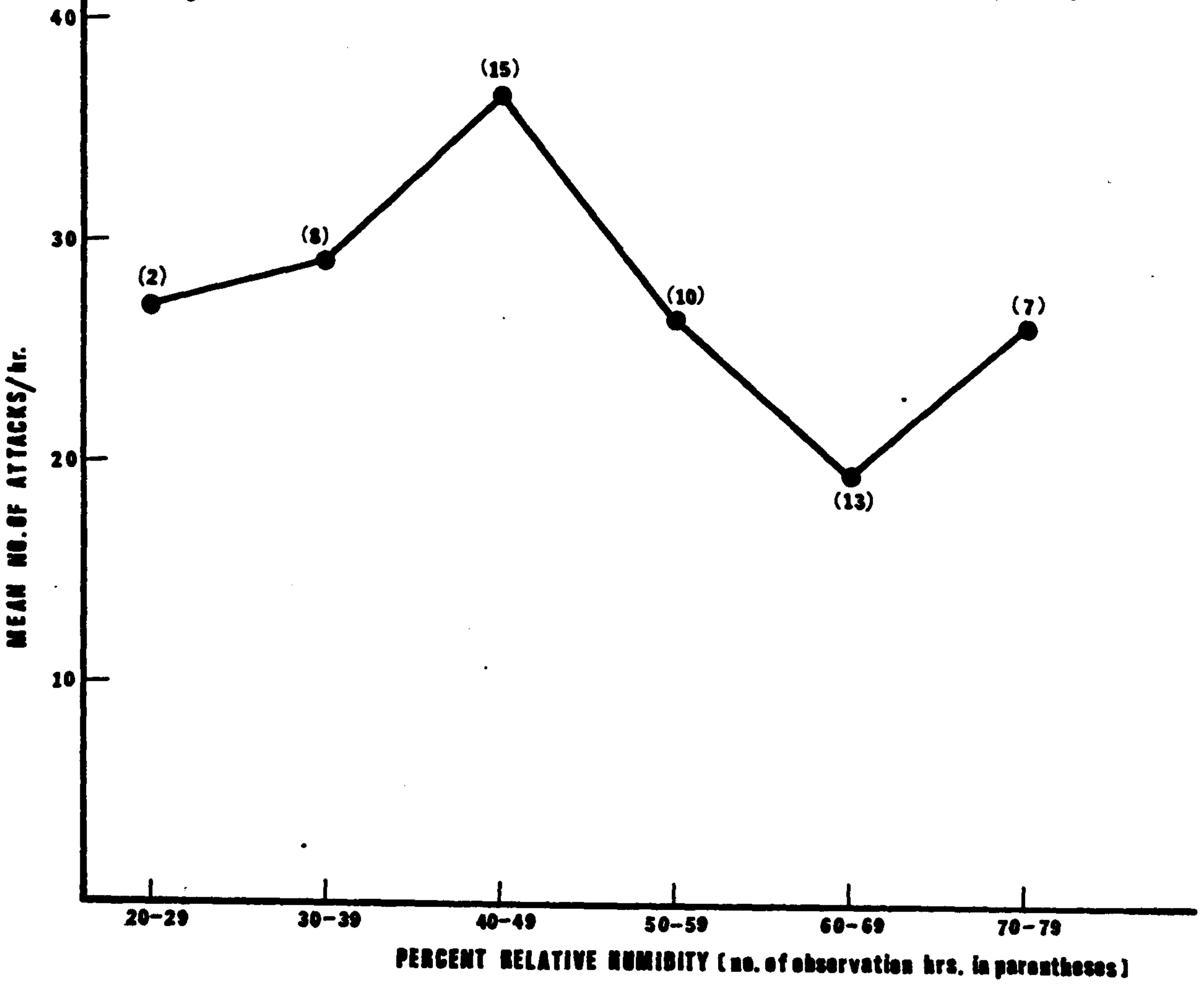
A dominance order emerged with two of the males clearly dominant over all of the other animals. These two males retreated whenever they came into contact with each other. The other two males and four aggressive females were dominant over all but the two most dominant

Table 13. Frequency of attacks as a function of temperature in high density population

Temperature	17-20° C	21-24° C	24-29° C
No. of observation hours	21 hrs	28 hrs	11 hrs
Frequency of attack	16.8 attacks/hour	29.2 attacks/hour	37.1 attacks/hour
Range	0-66/hour	0-73/hour	6-80/hour

Figure 7. Frequency of attacks with changes in relative humidity.

FREQUENCY OF ATTACKS AS A FUNCTION OF RELATIVE HUMIDITY.



animals. These six individuals were usually ignored, but were occasionally attacked, by the two most dominant males. It is probably significant that the four dominant males had all been caged together for several months prior to this study. The other fourteen males were the victims of severe attack by the eight dominant gerbils. They never attacked any animal, lost weight, were badly wounded, and remained huddled together. Whenever one of these "outcasts" left the huddle for food or water, it was attacked. Huddling together, therefore, seemed to decrease the probability of attack. It also resulted in an accumulation of feces and urine under the animals, themselves, which is unusual for this species. Occasionally one of the dominant gerbils would approach the huddle and "threaten" by digging at the substrate and making jerking movements. This resulted in the dispersal of the subordinate animals. The dominant gerbil would then chase one of them, biting him repeatedly. When the attack was over, the "outcasts" gathered in their previous location. When they made contact with each other, it was common for pairs to rise on their hind legs with their forelegs in contact, in a boxing-like posture. This boxing was accompanied by a high-frequency "chirping" sound.

While the "outcasts" were present in the population, the two dominant males occasionally attacked the two males of intermediate status, but the latter usually moved freely in and out of the nests of the former. It was only after the final "outcast" died that these two were severely attacked and killed. Finally, one of the remaining dominant males attacked and killed the other.

As previously mentioned, only four females were consistently involved in attacking other animals. These four had been caged together prior to their release into the enclosure. One of them was never observed attacking another gerbil until she was nursing her first litter, and then only when certain of the other gerbils entered or approached her nest. She drove the intruder away from the nest and on these occasions would sometimes attack other animals also. There were, however, certain gerbils which were permitted to enter and leave her nest without attack. These included one of the dominant males and two of the other dominant females.

An order emerged in which particular gerbils were singled out for attack. The first group consisted of the males other than the four dominant ones which had been cage-mates prior to being placed in the enclosure. Next were the smaller of the dominant males which never attained the level of dominance or aggressiveness of their larger cage-mates. When all other males were gone, the remaining two confronted each other, resulting in the survival of only one. The next group of gerbils to be attacked were those females which had nested with the defeated dominant male before his death. These, together with some females from the surviving male's "harem" formed a second group of "outcasts" which huddled together and behaved in a manner similar to the "outcast" males. When these female "outcasts" were killed, the dominant male began to attack and ultimately killed three of the high-ranking females. The sole survivor was the only female which became pregnant during the course of the study, and was the only female to successfully rear young.

The dominance hierarchy described here was formed early in the investigation and presumably was determined by direct confrontation between unfamiliar animals. Mutual fighting soon gave way to one-way attacks of dominants on subordinates. Most encounters considered aggressive consisted of very rapid chases, some of which never ended in contact. When an attack was "successful," it was usually only one to five seconds in duration and involved biting the base of the tail or the portion of the back just above the tail (since the animal attacked was always retreating). This method of attack resulted in severe wounding only because of its very high frequency. As more and more animals died, however, the dominant male and one of the females became very efficient killers. They held onto the subordinates which were in very poor condition by this time, and maintained their hold for as long as ten minutes while the legs were gnawed at and broken. The last animals to die all had at least one broken leg, and were sometimes missing a leg entirely.

Other patterns of social organization and behavior, not necessarily related to fighting, are worthy of mention. First, the dispersion of individuals can be described as follows. The two most dominant males nested at opposite corners of the enclosure. They would occasionally move to the other side of the enclosure, but would never enter each others' nest or directly confront one another. One of the male's had a "harem" of ten females nesting with him, while the other had seven in his nest, although he spent most of his time sleeping on top of the nest. One female usually nested by herself, and the outcasts huddled at a point half-way between the nests of the two dominant males and their "harems." These subordinate animals had no cover or accumulation of nesting material around them, whereas both of the other groups were usually under cover during their inactive periods. Possession of a nest was, therefore, indicative of social status. Any movement on the part of the subordinates, including those involved in self-maintenance, would precipitate an attack. This probably accounts for the lack of nest-building and the accumulation of elimination products by these animals.

Another activity related to both sex and social status was skimming. Only three males and one female, all dominant animals, were ever observed performing this activity. The males skimmed much more frequently than the female, which conforms with Thiessen, et. al.'s observations (1970). When some of these gerbils themselves became subjects of attack, they were no longer observed to skim.

A behavior pattern resembling "herding" was practiced on a few occasions by the most dominant males when one of their females left the nest. At these times, the male circled around her and chased her back toward the nest. Mounting was another behavior pattern observed only in dominant males.

After the elimination of all but one pair of the gerbils and the three surviving young from their first litter, the population began to increase slowly. For a time all of these animals nested together without fighting and were relatively inactive during observation periods. Whenever two animals came in contact they "nosed" and sometimes sniffed each other. When an animal came in contact with the dominant male, however, the former usually groomed his head briefly with forefeet held against him in a defense-like posture. When certain individuals became sexually mature and were later attacked by the dominant male, as previously described, they no longer nested with the rest of the group but usually retreated to a far corner.

The social organization of the two low density populations is simpler to describe. In the first case, when the two pairs of gerbils were introduced into the enclosure, fighting was observed between all pairs of unfamiliar animals. By the third day all attacks were being made on one male by the other. During these first few days, each of the male-female pairs which had been caged together nested in opposite corners of the enclosure. After the death of one of the males, all three remaining gerbils nested together, were relatively inactive, and were not observed to fight.

In the second low density population, initiated with four cagemates, no fighting occurred initially and all four nested together. It was only after the sexual maturation of the first litter that one of the original females was attacked and driven from the nest. The same pattern emerged as in the high density population, with only one gerbil at a time being attacked, and all others coexisting and nesting together without apparent conflict. Again, one of the males founding the population became dominant and was responsible for all of the attacks. However, in this case the other founding male was tolerated by him but all three males in the first litter were killed after they became sexually mature.

Physiological Effects of Fighting

The mean weights of the paired adrenal glands, testes, spleen, and female reproductive tracts for the four groups of gerbils used in the paired encounters and the animals which died during the initial decline of the high density population are shown in Table 14. Because

Table 14. Organ weights (mgs) for experimental groups

Group	Number of animals	Spleen	Adrenals	Rep. Tract
Isolated Females	(18)	65.3 ± 14.0*	33.9 ± 4.7	144.2 ± 42.9
Group-reared Females	(20)	59.5 ± 12.0	27.9 ± 4.9	162.1 ± 61.1
High density Females	(16)	396.0 ± 165.5	31.7 ± 7.8	65.4 ± 12.0
Isolated Males	(12)	63.2 ± 14.4	39.4 ± 6.0	1366.6 ± 144.6
Group-reared Males	(18)	71.1 ± 30.8	35.2 ± 5.8	1239.7 ± 213.7
High density Males	(10)	331.1 ± 155.9	37.6 ± 3.0	891.5 ± 80.0

*Standard deviation

of the great variability in the weight of the animals, organ weights relative to body weight are given to provide a more meaningful comparison between groups (Table 15). Relative organ weights are calculated as a ratio or organ weight in milligrams to the last measured body weight (in grams). Tables 16 and 17 give the mean absolute and relative organ weights, respectively, for surviving control animals. Unfortunately, many of the controls, including all of the group-reared males, died as a result of extremely high laboratory temperatures which occurred over one week-end. The Mann-Whitney U Test (Siegel, 1956) was used to compare group means.

1. Adrenal glands

The same order of increasing relative size of the paired adrenal glands is apparent for both males and females. Group-reared animals have the smallest glands while animals from the enclosure have the largest. It should be pointed out that relative organ weights for gerbils from the population enclosure are minimum values for two reasons: (1) these animals were autopsied after having been dead for up to forty-eight hours, so that organ weight probably decreased from dessication; (2) body weights used were those last measured when the animals were alive. Since these gerbils lost weight progressively until their death, the true weight at the time of death would be somewhat lower than the last measured weight. These two factors would tend to increase the value of the numerator (organ weight), and decrease that of the denominator (body weight), giving larger values than those listed in Table 15 for animals from the enclosure.

Statistically significant differences were found between isolated and group-reared females ($p < .05$), between group-reared and high

Table 15. Relative organ weights for experimental groups
[ratio of organ weight (mgs)/body weight (gms)]

Group	Number of animals	Spleen/weight	Adrenals/weight	Rep. Tract/weight
Isolated Females	(18)	0.789 ± 0.143*	0.417 ± 0.093	1.742 ± 0.480
Group-reared Females	(20)	0.746 ± 0.101	0.355 ± 0.074	2.035 ± 0.714
High density Females	(16)	5.590 ± 2.338	0.443 ± 0.104	0.920 ± 0.198
Isolated Males	(12)	0.646 ± 0.102	0.405 ± 0.043	14.130 ± 1.790
Group-reared Males	(18)	0.795 ± 0.292	0.398 ± 0.055	13.940 ± 1.690
High density Males	(10)	4.238 ± 2.115	0.480 ± 0.081	11.531 ± 1.302

*Standard deviation

Table 16. Organ weights (mgs) for control groups

Group	Number of animals	Spleen	Adrenals	Rep. tract
Isolated Females	(9)	71.6 ± 16.2*	33.3 ± 5.3	194.5 ± 40.5
Group-reared Females	(8)	65.4 ± 7.2	36.7 ± 5.9	203.1 ± 49.3
Isolated Males	(6)	66.5 ± 7.7	34.0 ± 2.5	1279.2 ± 127.1

*Standard deviation

Table 17. Relative organ weights for control groups [ratio of organ weight (mgs)/body weight (gms)]

Group	Number of animals	Spleen/weight	Adrenals/weight	Rep. tract/weight
Isolated Females	(9)	0.962 ± 0.143*	0.453 ± 0.081	2.644 ± 0.633
Group-reared Females	(8)	0.954 ± 0.083	0.543 ± 0.071	2.969 ± 0.727
Isolated Males	(6)	0.855 ± 0.155	0.432 ± 0.031	16.225 ± 0.330

*Standard deviation

density females ($p < .01$), between isolated and high density males ($p < .01$), and between group-reared and high density males ($p < .01$). On the other hand, group-reared female controls had significantly heavier relative adrenals than isolated female controls ($p < .025$) (Table 17).

2. Spleen

Both males and females which were killed in the high density population had tremendously enlarged spleens compared to both groups used in the paired encounters. This was apparent even upon gross examination. These differences were all significant beyond the 0.001 level of statistical significance. Differences in the relative size of the spleen between caged animals reared under different social circumstances were less spectacular, but nevertheless were statistically significant between isolated and group-reared males ($p < .025$). There were no significant differences between group-reared and isolated females, experimental or controls.

3. Reproductive tract

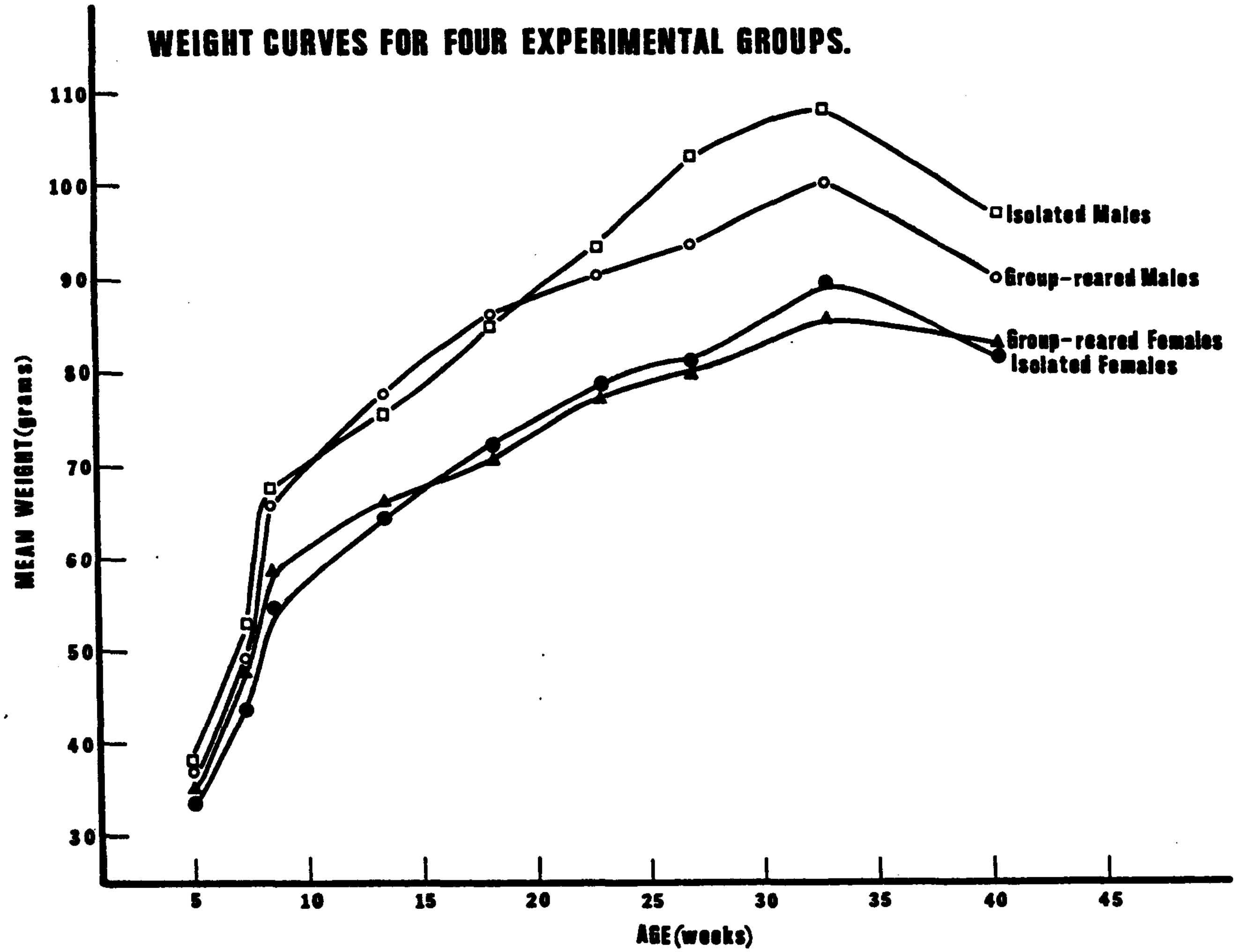
It can be seen in Table 15 that the order of increasing size of the female reproductive tract for the three groups is the inverse of that of the adrenals and spleen. High density females have significantly smaller reproductive tracts than either isolated or group-reared females ($p < .001$). Isolated females have smaller reproductive tracts than group-reared females (experimental and controls), but the differences are not significant ($p > .05$).

For males, the testes of high density animals are significantly smaller than those of caged gerbils ($p < .001$), but those of the two groups of caged males do not differ significantly.

For the three experimental groups of females, there is a direct relation between relative weights of the adrenals and the spleen, and an inverse relation between relative weights of the adrenals and reproductive tract. In males, too, those with the heaviest adrenals have the largest spleen and the smallest testes. This suggests that the relative weights of these organs may be related to the degree of fighting to which these groups of gerbils were exposed.

The weight record for the caged gerbils involved in the paired encounters (Figure 8) also indicates that fighting and/or being placed with unfamiliar animals is stressful. All four groups show the same rapid increase in weight which begins to level off somewhat with increasing age. Between thirty-three and forty weeks of age, however, all four groups show a distinct and unusual drop in mean body weight. This corresponds to the period during which the paired encounters took place.

Figure 8. Mean weight curves for the four experimental groups.



WEIGHT CURVES FOR FOUR EXPERIMENTAL GROUPS.

DISCUSSION

Paired Matches

1. Sex differences in behavior

One of the most striking differences in behavior in this experiment is that found between males and females. However, with only one exception, all the significant differences occur between individually-reared males and females. Individually-reared females significantly exceed males in fighting behavior by all four criteria, and also box and groom themselves more. On the other hand, individually-reared males show a higher frequency of digging and also many forms of non-fighting patterns of social interaction such as sniffing, investigating and grooming the chin and midventral gland, general grooming, and grooming the genitalia. It is apparent that sex differences are magnified by rearing the animals in social isolation, and the effect is to increase the level of female aggressiveness with corresponding drop in non-fighting social interactions compared to males.

The higher frequency of boxing among individually-reared females is related to the observation that boxing often occurs before and between fighting sequences. Self-grooming is probably a response to increased peripheral stimulation resulting from fighting and consequent wounds.

The only significant sex difference that appears between group-reared animals as well is investigation of the midventral gland. This greater male interest in this sebaceous gland corresponds with sexual dimorphism in the size of the gland. Thiessen, Friend and Lindzey (1968) reported a greater incidence of skimming by males and suggest that this is related to territorial behavior. Males in this study also skimmed more than females although the difference did not reach statistical significance. If this behavior and investigation of the gland were related to territoriality, one would expect that those showing a high frequency of these behavior patterns would be more "territorial," defined as a tendency to defend a territory, but in fact they fight less than females under the same conditions.

Generally speaking, only one sex difference appears between group-reared animals, while individually-reared males appear to be more interactive than females with respect to the other animal and the environment. Females seem to be more dependent on social experience for developing behavior which allows for intraspecific interaction without fighting.

2. Effect of the social group during rearing

Social deprivation during rearing has the effect of increasing the tendency to fight of both male and female gerbils. Fighting behavior of females is more affected by the social conditions under which they are reared than is the same behavior in males. Grouped females exceed individually-reared ones in the frequency of all forms of grooming and investigation, sniffing, and digging, while individually-reared females fight, box, nose, hip, defend, and groom themselves more frequently. Group-reared males show a greater amount of investigation and grooming the midventral gland and genitalia, and digging, while individually-reared males fight, box, hip, nose, and groom the chin more frequently.

It is apparent that the same treatment, social restriction, produces quantitatively different effects on different hormonal backgrounds. While grouped and individually-reared females show differences in the frequency of almost all the behavior patterns recorded, males have fewer significant differences in behavior with different methods of rearing. Both sexes, however, reveal the same qualitative trends as a result of isolation, namely an increase in all aspects of fighting and related behavior patterns such as boxing, hipping and defense, and a decrease in social investigation and grooming and environment oriented behavior (i.e., digging).

Social isolation produces a gerbil which shows less tendency to interact when placed in the proximity of another member of the species. It also shows less of certain non-interactive forms of behavior. This may indicate that, for the animal reared by itself, contact with another animal provides a strong conflict between approaching and withdrawing from the stranger. When contact is made, fighting frequently ensues since they are intensely aroused, never having had the opportunity to habituate to social interaction and develop responses which might preclude fighting.

3. Effect of the cage on behavior

The only behavior pattern which differed significantly between animals in their home and in other-home cages was digging. Group-reared males and females and individually-reared males all dug more in other-home than in their own cages. This is apparently stimulated by both the presence of another animal's odor and the absence of their own odor as there were no differences between home cages and neutral ones or between other-home or neutral cages.

A significant cage effect for individually-reared animals was the greater frequency of boxing by individually-reared females in neutral compared to other-home cages. Group-reared males and females, on the other hand, showed a higher frequency of fighting behavior and a lower frequency of several social investigative patterns in home and other-home cages than they did in neutral cages. Thus, the cage in which the match occurred was much more significant in determining the behavior of group-reared than it was for individually-reared animals.

A similar "home cage effect" on fighting has been described in other species (Davis, 1933; Uhrich, 1940; Ginsburg and Allee, 1942), and while this has sometimes been attributed to "territoriality," this explanation is not justified in the present study. If a greater degree of fighting in an animal's home cage represents a defense of territory, one would expect that there would be differences in fighting between the "territorial" (i.e., home) and the introduced (i.e., other-home) animal, or that the former would be the first to attack or would win the match more often. There were no significant differences between the two contestants in any of these measures (see Table 2, 3, and 4).

The signficant differences in behavior for group-reared animals is not between "home" and "non-home", but between "lived-in" and "non-lived-in" cages. As with sex and group differences, the inverse relationship between fighting and other forms of social interaction is apparent. The location of the match seems to affect the incidence of fighting through its effect on the rate of other forms of social interaction rather than through any direct effect of the cage itself.

The absence of many clear-cut cage effects on the behavior of individually-reared gerbils shows that group-reared gerbils are more influenced by their surroundings than are individually-reared gerbils. Possibly the presence of another animal is so strong a stimulus to a gerbil which has spent several months in isolation that it overrides any subtle effects of the cage in which it occurs. The frequency of fighting is high and the frequency of other social interaction low, regardless of the cage.

4. Effect of observational sequence on behavior

Only five behavior patterns showed any change in frequency with increased experience in the observational situation: approaching, sniffing, nosing, and investigation of the chin and midventral gland. The last three were also affected by the location of the match. All of these are brief forms of interaction. The obvious trend which appears in the data are the differences between individually-reared females and group-reared males. While the former show a decrease from the first to the third match in nosing, and investigating the chin and midventral gland, the latter increase the frequency of approaching, sniffing, and investigating the chin. These two groups are also at opposite ends of the scale in terms of fighting and other forms of interaction as well. Group-reared females are inconsistent in that they increase in the frequency of approaching and decrease in the frequency of investigating the chin. Individually-reared males are the only group which shows no significant sequential changes in behavior.

Overall, the effects of sequence in this study are small, and limited to particular forms of low intensity social interaction. While group-reared males become more interactive, individually-reared females decrease their tendency to investigate strangers, possibly as a result of negative reinforcement through prior fighting experience.

5. Correlations between attacking and other behavior patterns

Correlations were found between the frequency of attack and the frequency of several behavior patterns in group-reared males and females in other-home cages. These include hipping, defensive behavior, and investigating the genitalia in males, and hipping, boxing, grooming, investigating the genitalia, mounting, and foot-stomping in females. In home and other-home cages all four groups showed positive correlations with hipping. In neutral cages only individually-reared males and females did. This is because of the sharp drop in fighting behavior of group-reared animals in neutral cages.

For individually-reared gerbils, the significant correlations occurred rather randomly among the three cages, as might be expected since the frequency of attack did not differ significantly with the cage. Individually-reared males and females showed high positive correlations between attacking and hipping and boxing. Grooming was negatively correlated with attack in individually-reared males. Attack frequency in individually-reared females was positively correlated with self-grooming and digging, and negatively correlated with defensive behavior.

The only behavior patterns which are consistently correlated with attack across two or more groups (at least in one cage situation) are hipping, boxing, and investigating the genitalia. Boxing is an upright posture involving both animals which occurs before or between bouts of attacks. Hipping is an aggressive lateral posture which often precedes an attack. It shows the strongest relationship with attack of any of the behavior patterns. Investigating the genitalia' is correlated with attacking only for group-reared animals in other-home cages. This may indicate that odors from this area are a stimulus for attack and may be related to the cage differences in fighting and digging behavior in these two groups.

6. Confounding variables

Time of day, relative humidity, and cyclical hormonal changes were variables which were not controlled. However, encounters were arranged so that no group met consistently at the same time of day. In paired matches, time of day did not at all influence the probability of fighting. The sudden introduction of a strange gerbil must provide a strong stimulus which overrides any periodicity that might otherwise exist.

High relative humidity (above 59%) had the effect of slightly decreasing the incidence of fighting behavior. This species does not seem to tolerate higher humidity well, as is apparent from their general lethargy under these conditions. Since their native habitats are desert and semi-desert areas, they are probably not well adapted physiologically to high humidity, and this is reflected in their level of general activity.

No attempt was made to assess the importance of physiological factors such as variations of hormonal levels with the estrus cycle on fighting behavior. However, cyclical changes in the frequency of female fighting behavior were not apparent.

Population Dynamics and Aggression

If fighting serves an intrinsic mechanism for population control, then fighting should in some way be related to population density. Within single confined populations of house mice, aggressive activity increases with density, but it varied greatly between different populations, irrespective of density (Southwick, 1955a). I observed a similar relationship between density and fighting in confined laboratory populations of Meriones unguiculatus. Aggressive behavior, however, is not a simple linear function of density. Figure 4 indicates that the rate of attack varies considerably but remains at a high level despite a drastic decrease in number of animals. The rate drops sharply only when the population density reaches six animals in fifty square feet. It appears that fighting occurs when an "excess" number of animals is present and ceases when they are gone. Within these limits, frequency of attack is not directly related to density. This may be due to the relatively few animals involved in attacking. If fighting occurred between all individuals, the rate of fighting would decrease as numbers decline because of the fewer possible combinations of individuals. There is a more direct relationship between density and aggressive activity, however, when sex-specific density is considered (see Figures 5 and 6). Hence, attack is not entirely random.

The order in which specific animals or groups of animals are singled out for attack can be described in terms of an increasing level of threshold for attack on the part of dominant males. The lowest threshold of response occurs for unfamiliar animals of the same sex; the next highest level for familiar gerbils of the same sex; then unfamiliar animals of the other sex; and finally, familiar gerbils of the other sex may be attacked. It is only after the elimination of all of the individuals on the previous level that the next group comes under attack.

Females are less discriminating in terms of which animals they attack. Their aggressiveness is also more sporadic. Aggressive females may go for several days without any attacks being observed, and then they may become highly aggressive. No cyclical pattern was apparent, however. From the behavior of the female which successfully reared young in the high density population, it seems that defense of young is part of the behavioral repertoire of this species. Strange animals were attacked and driven from the nest while the pups were being nursed, although this female was never previously observed fighting. This behavior may have contributed to her success in rearing her young. Familiar gerbils, on the other hand, were permitted to enter the nest. Defense of the nest and young by the lactating mother was never observed in the low density populations, perhaps because there were never any unfamiliar animals present.

Of the several possible kinds of dominance hierarchies described in rodents, the one which most closely resembles that found in _M. unguiculatus_ has been described for rats by Barnett (1963). The dominant males and females in this study correspond to his _alphas_, those of intermediate status to _betas_, and the "outcasts" to his _omegas_. This type of dominance order, however, is of short duration. Some of the _betas_ become _omegas_, and the _omegas_ are soon eliminated from the population. A more commonly described type of dominance relationship then emerges with one dominant male and all others having equivalent status. It is difficult to determine a dominance order in the absence of fighting, however, since there is no visible competition for resources or for nest sites. Only subtle differences in behavior were observed. For any given subservient individual, the method of "greeting" peers differed from the way in which the dominant male was "greeted." Peers were freely sniffed and groomed when contact occurred, but the dominant animal was nosed and/or the defensive posture was assumed for a short time. The dominant male investigated and sometimes groomed his subordinates.

There can be little doubt that under the conditions of this experiment, aggressive behavior directly affects population density. All but one of the adult animals which died bore wounds. Although these wounds may not necessarily have been the immediate cause of death, if death resulted from disease, only those bearing wounds were susceptible. The rapid decline of the high density population and the death of one male in the first low density population are attributable to fighting.

The possibility exists that fighting could be the result of the artificial conditions of the experiment. Throwing a large number of unfamiliar animals together under confined conditions might produce aberrant behavior patterns. Brown's (1953) results indicate that such artificially assembled populations of mice also exhibit intense and prolonged fighting, while naturally growing ones do not. In the present study, the high density population was at first artificially assembled, while the second low density population was naturally growing. Brown's findings for mice are paralleled by only the early history of each of these two gerbil populations.

While the initial turmoil in the high density and in the first low density population may have resulted from the presence of strange animals, this is evidently not the whole explanation for fighting. First of all, aggression was not limited to strangers; former cagemates were attacked as well. Secondly, in the high density population, there was a six-month period in which aggression was entirely absent. When it began again, it was directed towards the dominant males' own offspring which were reared in his presence. In the growing low density population also, after an initial period completely free of aggressive interactions, fighting began with the maturation of the first litter. In this case it was directed toward one of the founding females.

The pattern of emergence of fighting in both populations supports the hypothesis that fighting and density are causally related. In the high density population, the re-emergence of fighting was first observed about four weeks after the sexual maturation of the fourth litter, when the number of adults reached thirteen. It continued with one animal at a time being attacked until the population fell to seven. In the second low density population, fighting began five weeks after the maturation of the first litter, when there were eight adults present. It stopped after the death of one female and began again about two weeks after the maturation of the survivor of the second litter, when there were again eight adults in the population. This time it continued until the number of adults dropped to four.

Aggression appears to be a behavioral method of population self-regulation in M. unguiculatus. This behavior has been shown to be highly reactive to density of the adult population. It is significant that despite the very different levels at which the two experimental populations were begun, both leveled off nearly the same density. Food and water were never limiting factors. It can be concluded that under the limitations of space, environmental complexity, and confinement of this study, a population of not more than seven or eight adults is tolerable, and probably four or five is ideal. It is not known what parameters of density stimulate fighting, nor why particular individuals are selected for attack. While the attacking of "excess" individuals is performed by the dominant animals, this does not necessarily mean that removal of animals high in the dominance hierarchy would eliminate fighting. It is likely that most gerbils are potentially aggressive, but this tendency is inhibited by their subordinate role.

A question arises as to why a similar kind of pattern does not occur within cages. Many of the animals used in the population study had been kept under conditions of considerably higher density prior to their release into the enclosure, without any evidence of fighting. It was only after release into the larger area that fighting began. It is likely, therefore, that a minimum area is required before members of this species display certain behavior patterns. Whether or not these are related to territoriality depends on how territoriality is defined. Thiessen and his colleagues (1970) have suggested that the skimming response is territorial in nature. I have no hard evidence to support this hypothesis, but it is noteworthy that this behavior is only displayed by dominant gerbils, particularly males. While two dominant males were present in the high density population enclosure, there was a clear delimination of the area into separate "territories." The settling of the outcasts at the half-way point between the nests probably minimized the probability of attack by either dominant male. From later events, however, it is apparent that the enclosures could support no more than one dominant male and probably only one breeding female. Lactating females seem to defend the area around their nest and may at times participate in the defense of the larger "group territory." The area in the enclosure seems adequate for a group of not more than eight adults with not all of these actively breeding.

While laboratory and field populations are not strictly comparable, it is tempting to speculate on the significance of these results to population dynamics of gerbils in the wild state. Under natural conditions these animals are burrowers (Tanimoto, 1943), and it is likely, therefore, that a higher density could be supported in a system of burrows than on a flat substrate. Burrows would reduce the frequency of contact between animals and would increase the amount of cover available for escape. Since confinement is highly artificial, it is unlikely that attacks in the natural environment would ever result in the death of subordinate animals. If the social structure observed during the course of this investigation is also typical of that in the natural habitat, it can be assumed that fighting begins with the sexual maturation of young animals. This would tend to drive out either these individuals or possibly older, submissive gerbils. This points out the possible significance of subordinate animals in the evolutionary process, recently stressed by Christian (1970).

Animals driven out of their family group might be able to set up their own burrow system outside of the territory of the former.

If the surrounding areas were occupied by other groups, however, it is unlikely that these strange, submissive animals would be permitted to settle there. They would, therefore, be forced to move to unoccupied areas. This would create a series of adjacent territories, each occupied by a small group of related animals. Aggressive interactions would keep the groups distinct and disperse surplus individuals from the group territory. When all suitable habitat was occupied, additional animals might be killed, or would be driven into marginal areas where their chances for survival would be reduced.

Aggression then, is a behavioral mechanism with the potential for regulating the population organization and density of M. unguiculatus. There is evidence, however, that it is not the only way this species can limit its numbers. Consideration of the birth and survival records of young born during the course of the study (Tables 11 and 12) shows that both the number of offspring born and the proportion surviving is far below the reproductive potential of gerbils. One reason for this was that very few breeding females were present in either population. It is not known whether this was the result of physiological or behavioral factors, or both.

No female which died as a result of attack was found to be gravid. Therefore, only those females which successfully reared litters are known to have conceived during the course of this study. The observed atrophy of the reproductive tract of dead females may account for the limitation of breeding in the population enclosures. Moreover, high density and agonistic interactions may interfere with the estrus cycle, and females may even go into periods of prolonged anestrus (Eisenberg, 1967; Chitty and Austin, 1957). Lloyd and Christian

(1969) also found that only a limited number of females in three experimental populations of house mice were reproductively active and that this was related to their social rank and to population density.

Breeding is much more prolific in cages than it is in a colony situation. The initial unsuccessful litters in the high density population enclosure all resulted from matings which took place in cages. Those litters were either not nursed, were scattered, or were cannibalized, and no other pregnancies occurred in these females. This was not directly attributable to attacks upon females because these did not begin for about two months after their release. The fighting and social instability characteristic of the first few months in the enclosure were not conducive to successful reproduction.

In addition to the failure of the vast majority of females to conceive, poor litter survival is another population-limiting factor which appears to be related to density in this study. The percentage surviving to weaning is somewhat related to the number of adults present in the population at the time of parturition. In the high density population, the first successful litter was born when the number of adults was twenty-two. In this case 50% survival was possible because the mother was able to keep other animals out of her nest. As the number of adults decreased to a much lower level, the survival rate increased. After the population began to increase once again, none of the litters survived. There followed a period of several months without any more young being born. A similar relationship between litter survival and adult density existed in the low density population. While some of the pups were found half-eaten or were not found at all, the majority of them died without injury. It is likely, then, that density somehow affects the physiology of lactation of the mother. This may occur at the level of the pituitary through increased production of ACTH at the expense of lactogenic hormones. Christian (1963) also noted a marked decline in litter survival with increasing density. In populations of house mice, destruction of litters by killing or abandonment was the most significant block to population growth (Brown, 1953).

The adaptive value of such intrinsic population limiting mechanisms, if they do exist in natural populations of M. unguiculatus, is obvious, particularly in a desert habitat where resources are quite limited. In populations where such mechanisms are absent or inoperative, density increases to a point at which resources become limiting and starvation ensues (Elton, 1933; Krebs, et. al., 1969).

Physiological Correlates of Fighting

1. Adrenal glands

The adrenal glands have long been implicated in reaction to stress in animals. Selye's (1946) "General Adaptation Syndrome" (GAS) consists of three phases: (1) the alarm reaction in which the adrenal cortex is depleted and there are symptoms of shock and hypoglycemia; (2) the resistance phase in which the adrenal cortex is hypertrophied and resistance to stress is acquired at the expense of the ability to adapt to any additional stress; and, (3) the exhaustive phase in which the adrenal cortex is hypertrophied with depletion of its secretory products. In this last phase the animal is no longer able to maintain its resistance and dies if stress continues.

The results of the study reported here fit into this theoretical framework. It can be hypothesized that the isolated, caged animals, particularly the females, were in the resistance phase at the time of sacrifice, while those which died in the population enclosure were in the exhaustive phase. It is perhaps significant that while not a single experimental animal died in the eight months preceding the paired encounters, five died in the six-week period following the initiation of the experiments. It is possible that the stress of the experimental procedure and/or fighting, made them less resistant to some infectious agent. Further evidence that the experimental procedure was stressful comes from examination of the weight records (Figure 8). While all four groups show a normal growth curve with increasing weight leveling off with age, there is a significant and abnormal mean weight loss during the time when individuals were involved in paired matches.

The same explanation would apply to the proximate cause of death of the gerbils in the high density enclosure. While all of these animals were extensively wounded, the wounds were superficial and none penetrated any vital area. Therefore, no gerbil can be said to have died directly from injury. High density has been found to enhance mortality in several ways. Death from "shock disease" can occur after a prolonged period of social stress (Frank, 1957; Christian, 1955a). Animals may also die,,not directly from fighting, but from infection and parasitism of wounds (Eisenberg, 1967; Louch, 1956; Southwick, 1955b). Animals from high density populations seem to be more susceptible to disease than those from populations of lower density (Louch, 1956). The most plausible hypothesis is that a combination of the effects of stress from the continuous attacks and inanition brings them into the resistance phase of Selye's GAS, and they are therefore more susceptible to other stressful factors. Evidence for this also comes from the increased relative adrenal weights of these gerbils since cortisone, hydrocortisone, and corticosterone suppress the inflammation response and the formation of antibodies, and this increases the pathogenicity of various organisms (Christian and Davis, 1964; Christian and Williamson, 1958).

The question arises as to what constitutes stress for an animal. Christian and his colleagues have found a direct relationship between the amount of adrenocortical tissue and population size in both white and wild house mice in confined populations (Christian, 1955b; Davis and Christian, 1957). What is it about population density that is stressful? Limitation of food did not lead to adrenal hypertrophy in mouse populations (Christian, 1959a). Christian (1959b) says that fighting <u>per</u> <u>se</u> doesn't account for adrenal hypertrophy because the latter apparently occurs in populations without fighting; because dominant animals which fight at least as much as subordinates do not show this condition; and because he found no relationship between injury from fighting and adrenal weight. He concludes that the basic stimuli for the endocrine changes are socio-psychological, or "emotional," but he does not elucidate what these stimuli are (Christian and Davis, 1964; Christian, 1963).

The hypertrophy of the adrenal glands found in this study supports the hypothesis that fighting is an important stress factor in <u>M. unguiculatus</u>. The relative adrenal weights (Table 16) increase for both males and females in the following order: (1) group-reared,

(2) isolated, (3) high density population. This is related to the relative amount of fighting since group-reared gerbils fought the least, while those in the high density population enclosure were subjected to the most fighting. The order of increasing adrenal size is not related to density in the experimental groups, but in the controls, group-reared females showed hypertrophy compared to those females reared by themselves. It is possible then that fighting is the most important form of stress contributing to adrenal hypertrophy in this species. Hypertrophy is not limited to subordinate animals since there were no significant differences between animals characterized as winners and losers in the paired matches. Females show a more pronounced difference in relative adrenal weight than do males. A similar sex difference in adrenal response was found for *Peromyscus maniculatus* (Terman, 1969). It seems then that the adrenals of females are more responsive than those of males to social stimuli.

Other workers have found a direct relation between amount of fighting and adrenocortical activity. According to Clarke (1952), subjection to attack led to pronounced increase in adrenal weight in voles. He also found that the direct cause of increased adrenocortical activity with high population density in *Microtus pennsylvanicus* was the higher incidence of fighting that occurred in his experimental pens during periods of high density. Rats living in groups in which fighting took place had adrenals about one-third larger than animals living under peaceful conditions. This applied to both dominant and subordinate animals (Barnett, 1958b). In another study, the adrenal cortex of subordinate rats involved in severe fighting over short periods (two days) showed marked depletion of sudanophilic materials.

Dominants did not show a similar effect (Barnett, 1955). Relative adrenal weight increased progressively during eight days of brief exposure to fighting in trained fighting mice (Bronson and Eleftheriou, 1965a). Archer (1970) found that success in aggressive encounters, in contrast to defeat, did not result in increased adrenocortical function in laboratory mice. In Peromyscus leucopus, grouped animals showed no adrenocortical response when they were "compatible" but did if they were "incompatible" (Southwick, 1964). Southwick and Bland (1959) found an increase in relative adrenal weight in wounded animals.

The importance of psychological factors to adrenal size was demonstrated by Bronson and Eleftheriou (1965b). The concentration of unbound corticosterone in house mice exposed to the presence of a trained fighter was much greater if mice had previously experienced physical defeat than if they had not. There was little difference in the concentration of hormones between mice placed in the presence of a fighter and mice actually attacked and defeated if both had previously experienced physical defeat. Placing isolated mice in strange cages can in itself affect adrenocortical activity (Southwick, 1959).

Adrenocortical function appears to be very sensitive to social interaction regardless of the effects of density. Mice housed in adjacent wire mesh cages had heavier adrenals than those separated by wooden partitions (Archer, 1969a). This effect is probably due to olfactory stimuli, since exposure to the odor of other males alone can also produce hypertrophy (Archer, 1969b). Male rats in mixed colonies had larger adrenals than those in all-male colonies and controls in small cages (Barnett, 1958b). That density is not the only factor involved is also indicated by studies in which isolated animals were found to have heavier adrenals than grouped animals (Bronson and Chapman, 1968; Wiberg and Grice, 1963). Even the work of Christian and his associates shows certain inconsistencies on the question of density. For example, albino mice reached peak adrenal weight with increasing density followed by a decline as the population increased further. That this may be related to fighting is indicated by the fact that "the bulk of the mice in these larger populations [above the level of peak adrenal weight] got along amicably" (Christian, 1955a). Ghosh, *et*. *al*. (1968), studying the Indian desert gerbil, *Meriones hurrianae*, also found an increase in adrenal weight for one, two, and three animals per cage, respectively, followed by a decrease for four animals per cage.

Many of these apparently conflicting results can be accounted for if one considers the previous history of the animals used in the experiment. For example, Christian (1959a) took mice which were segregated from weaning and placed them in different size groups for a week. The adrenal weights were proportional to the size of the group. There is little doubt that placing isolates in contact with other animals is stressful. Wiberg and Grice (1963), on the other hand, started with rats reared in community cages and placed them in isolation for three weeks, with the result that the isolated rats had heavier adrenals than those left in community cages. One should also be aware of the developmental history of the animals. Stress may result from a drastic change in the environmental conditions rather than from density *per se*.

The observed relationship between fighting and relative adrenal size can be explained in one of two possible ways: (1) fighting causes adrenal hypertrophy, or (2) the experimental conditions themselves produce hypertrophy and the accompanying increased level of circulating adrenocortical hormones lower the threshold for fighting. Certainly other hormones (e.g., androgens) are known to affect this threshold in other species (see pp. 22-25). This might account for the greater incidence of fighting among isolates. However, those animals with the largest adrenals were those killed in the high density population enclosure which did no attacking at all. Furthermore, control females which were not involved in any fighting showed the reverse order, with isolates having smaller adrenals than group-reared animals. One would have to conclude, therefore, that the relative size of the adrenals is a consequence rather than a cause of fighting in the experimental groups.

2. Reproductive organs

Examination of Table 15 reveals that there is an inverse relationship between relative adrenal weight and the weight of the female reproductive tract. Females killed in the enclosure had significantly smaller reproductive organs than either group of caged females. A similar relationship between atrophy of the female reproductive tract and increased adrenocortical activity has been found by Christian (1960). Physiological effects on the female reproductive organs, therefore, may be an additional means of population regulation in <u>M. unguiculatus</u>. It will be recalled that, in the enclosure, none of the females gave birth or was known to conceive. Lowered fertility and a reduced number of pregnancies can result from a variety of causes related to density and agonistic behavior. Estrus cycles may be interfered with and females may go into periods of prolonged anestrus (Eisenberg, 1967; Chitty and Austin, 1957). Lowered fertility resulting in cessation of reproduction with increasing density has been found in Mus (Crew and Mirskaia, 1931; Crowcroft and Rowe, 1957; Strecker and Emlen, 1953), in Peromyscus maniculatus (Terman, 1969), and in Rattus(Barnett, 1967b). Barnett (1964) believes that the most important effects of mutual intolerance in mammals are those involving the female reproductive tract. This type of effect may also account for the population cycles in small mammals such as voles and lemmings (Chitty, 1960).

Selye (1950) suggested that activities such as growth, reproduction, and lactation, which are not immediately necessary for the maintenance of life during an emergency, are inhibited because of a shift in the activity of the anterior pituitary toward ACTH at the expense of the production of gonadotrophic, growth, and lactogenic hormones. On the other hand, cortical steroids may have a direct effect on the reproductive tract. The evidence in the present study suggest, however, that environmental stimuli exert a separate influence over adrenals and female reproductive tract since in the controls, the relative weights of these organs were directly related.

An inverse relationship also exists for males, but not to the same extent. Males from the high density population had significantly reduced testicular weight compared to isolated and grouped males which did not differ significantly from each other. Again, the physiological effects of social stimuli are not as great in males as in females.

3. Spleen

Weight of the spleen is not clearly related to relative adrenal weight in caged animals, but there is a highly significant difference between the spleens of caged gerbils and those which died in the enclosure. The latter also had the largest relative adrenal size. Clarke (1952) has found that fighting increases the weight of adrenals and spleen in Microtus. As previously mentioned, adrenocortical steroids suppress inflammation and the formation of antibodies. The increased weight of the spleen may indicate a weakened condition which enables pathogens to become invasive. Chitty (1957) found gross splenic hypertrophy in field-caught voles as compared to laboratory animals. The largest spleens occurred in the densest breeding populations, and Chitty believes that this condition is related to their subsequent decline in numbers. Hemolytic anemia, but no infectious agent, was found to be associated with this condition. A more thorough analysis of the possible pathological causes of this gross splenic hypertrophy might be a fruitful area for future investigation.

SUMMARY

1. Male and female gerbils (Meriones unguiculatus) were reared either singly or in unisexual groups of five for eight months after weaning. They were then paired three times (in their home cage, in another gerbil's cage, and in a neutral cage) with like-sex strangers of the same rearing condition for twenty minutes. Recordings were made of fight and attack frequency and duration, fight latency, and the frequency of nineteen other behavior patterns.

2. Individually-reared females were more aggressive than individually-reared males by all four criteria, but group-reared females were slightly, but not significantly more aggressive than group-reared males.

3. Sex differences in other behavior patterns are also magnified by social deprivation. While group-reared males and females differed significantly in only one behavior pattern, individually-reared males and females differed in several. Males were more often involved in social investigation while females scored higher in behavior patterns related to fighting.

4. Gerbils reared individually were significantly more aggressive than group-reared animals of the same sex.

5. Social isolation had the effect of decreasing the frequency of non-fighting forms of social interaction and increasing fighting and related behavior patterns in both sexes. Larger differences were produced in females than in males as a result of rearing condition.

6. The cage in which the match occurred did not affect the amount of fighting or other behavior in individually-reared animals, but

group-reared males and females fought more in home and in other-home than in neutral cages. They also showed a lower frequency of social investigative patterns in lived-in cages.

7. Only a few behavior patterns, all forms of brief interaction, were significantly affected by the observational sequence. Individually-reared females decreased, while group-reared males increased, the frequency of these patterns with experience. Individually-reared males were not affected by observational sequence.

8. Behavior patterns found to be significantly correlated with the frequency of attack in more than one group were hipping, boxing, and investigating the genitalia. Defensive behavior was negatively correlated with attack.

9. Time of day and relative humidity did not effect the tendency to fight. Relative weight of the contestants did not affect fight outcome.

10. The first animal to attack in a match was most often the winner of the match.

11. The pattern of results showed a general consistency between consequtive matches for individual animals.

12. The social organization and population dynamics of two confined populations were studied for a period of sixteen months. The "low density" population was begun with two pairs, and the "high density" population with eighteen pairs of gerbils.

13. The social organization within these two populations is described. A dominance hierarchy was observed with one dominant male and all others having equal status.

14. Fighting was found to be related to the number of adults present in each population. The largest tolerable number of adults at any time was eight. Fighting emerged with the sexual maturation of each litter and stopped when the number of adults was again reduced as a result of fighting.

15. Litter frequency and survival rate were also related to the number of adults in the population.

16. A limited number of females successfully bred during the course of the investigation.

17. Weights of adrenals, spleen, testes, and female reproductive tract were measured for gerbils used in the paired matches, their controls, and those killed in the high density population.

18. Relative adrenal weights were directly related to the amount of fighting the group was involved in, but not to density. Controls, which were not exposed to fighting or to strangers, showed hypertrophy in the grouped situation as compared to isolates.

19. Females showed more pronounced adrenal responses to social stimuli than males.

20. Gross differences in spleen size were found between caged gerbils and those killed in the population enclosure.

21. Relative weight of the female reproductive tract was inversely related to the amount of fighting and relative adrenal weight in the experimental groups.

22. It is suggested that fighting behavior, birth rate, survival of young, number of breeding females, and changes in organ weights are factors which may all curtail population growth in *M. unguiculatus*.

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APPENDIX

Medians and ranges for all groups for all behavior patterns within both observational sequence and cage

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Fighting	GM	N*= 6 0 0 - 5	N = 4 10 0 - 26	N = 10 0 0 - 5	N = 6 0 0 - 5	N = 4 0 0 - 26	N = 10 0 0 - 5	N = 8 0 0 - 0	N = 12 0 0 - 0
	GF	N*= 6 0 0 - 7	N = 6 0.5 0 - 3	N = 12 3 0 - 25	N = 6 0 0 - 7	N = 6 0.5 0 - 3	N = 12 3 0 - 25	N = 12 0 0	N = 12 0 0 - 10
	IM	N*= 2 0 0 - 0	N = 3 1 0 - 6	N = 5 0 0 - 4	N = 2 8.5 0 - 17	N = 3 1 0 - 6	N = 5 0 0 - 1	N = 6 2 0 - 14	N = 4 2 0 - 3
	IF	N*= 5 9 3 - 22	N = 4 1.5 1 - 2	N = 9 7 0 - 88	N = 5 9 3 - 22	N = 4 1.5 1 - 2	N = 9 7 0 - 88	N = 8 27.5 0 - 45	N = 10 12 6 - 54

*Number in each group remains the same throughout

GM = Group-reared males

GF = Group-reared females

IM = Individually-reared males

IF = Individually-reared females

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Attacking	GM	0 0 - 4	10 0 - 26	0 0 - 5	0 0 - 2	0 0 - 0	0 0 - 5	0 0 - 0	0 0 - 0
	GF	0 0 - 0	0.5 0 - 1	2 0 - 25	0 0 - 7	0.5 0 - 2	0 0 - 25	0 0 - 0	0 0 - 10
	IM	0 0 - 0	0 0 - 3	0 0 - 4	8.5 0 - 17	1 0 - 4	0 0 - 1	0 0 - 14	0.5 0 - 3
	IF	7 3 - 22	0.5 0 - 2	4 1 - 21	1 0 - 7	1.5 0 - 2	2 0 - 88	1 0 - 44	3.5 0 - 54
Time spent fighting (sec)	GM	0 0 - 50	29 0 - 77	0 0 - 53	0 0 - 50	0 0 - 77	0 0 - 53	0 0 - 0	0 0 - 0
	GF	0 0 - 17	2 0 - 8	5.5 0 - 76	0 0 - 17	2 0 - 8	5.5 0 - 76	0 0 - 0	0 0 - 47
	IM	0 0 - 0	1 0 - 18	0 0 - 11	82.5 0 - 165	1 0 - 18	0 0 - 11	8 0 - 119	40 0 - 81
	IF	68 42 - 105	4 1 - 27	46 0 - 140	68 42 - 105	4 1 - 27	46 0 - 140	53.5 0 - 150	77 11 - 134

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Fight latency (sec)	GM	cbd* 307 - nf**	cbd 61 - nf	cbd 88 - nf	cbd 307 - nf	cbd 61 - nf	cbd 88 - nf	cbd nf	cbd nf
	GF	cbd 119 - nf	258.5 517 - nf	686 22 - nf	cbd 119 - nf	258.5 517 - nf	686 22 - nf	cbd nf	cbd 313 - nf
	IM	cbd nf	82.5 139 - nf	cbd 778 - nf	cbd 818 - nf	82.5 139 - nf	cbd 778 - nf	49.5 32 - nf	737.5 517 - nf
	IF	537 215 - 892	1179 2 - 1200	289 1 - nf	537 215 - 892	1179 2 - 1200	289 1 - nf	151 2 - nf	553 67 - 892
Investigating the chin	GM	2 1 - 11	1 0 - 2	0.5 0 - 6	3 1 - 13	3.5 2 - 6	0.5 0 - 3	3.5 1 - 11	4.5 1 - 13
	GF	5 1 - 8	2 0 - 5	1 0 - 4	1.5 0 - 8	2 1 - 6	1 0 - 3	3 0 - 7	3 2 - 9
	IM	1 1 - 1	1 0 - 5	2 1 - 6	6.5 6 - 7	2 0 - 13	1 1 - 4	1 0 - 12	2.5 1 - 5
	IF	3 2 - 6	0 0 - 4	0 0 - 5	4 0 - 7	3 1 - 4	0 0 - 1	1 0 - 7	1 0 - 8

*cbd = cannot be determined

**nf = no fight; total observation = 1200 sec

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Investigating the midventral gland	GM	2.5 2 - 5	3 1 - 8	1 0 - 4	1 0 - 5	2 1 - 6	0.5 0 - 3	5 1 - 19	6.5 0 - 18
	GF	3.5 3 - 6	0.5 0 - 10	1 0 - 7	1 0 - 4	1 1 - 3	0.5 0 - 3	3 0 - 14	2.5 0 - 11
	IM	0.5 0 - 1	0 0 - 0	0 0 - 2	2 1 - 3	1 0 - 1	0 0 - 2	1 0 - 4	1 1 - 3
	IF	1 0 - 8	0 0 - 0	0 0 - 1	1 0 - 2	0 0 - 0	0 0 - 0	0.5 0 - 1	0 0 - 3
Investigating the genitalia	GM	4 3 - 13	1.5 0 - 4	3 0 - 11	4 2 - 6	2.5 0 - 3	1 0 - 8	6 0 - 10	5 0 - 16
	GF	9.5 2 - 13	2 0 - 9	2 0 - 20	1.5 1 - 21	2 1 - 5	2.5 0 - 9	7.5 0 - 18	6 1 - 12
	IM	5.5 3 - 8	0 0 - 0	0 0 - 14	5.5 5 - 6	0 0 - 1	0 0 - 2	2 0 - 13	0 0 - 1
	IF	1 0 - 5	0 0 - 0	0 0 - 2	0 0 - 0	0.5 0 - 1	0 0 - 0	0 0 - 1	0 0 - 2

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Grooming	GM	9 3 - 20	3 2 - 12	12 3 - 25	8.5 8 - 17	9.5 7 - 14	8 2 - 22	9.5 1 - 31	10.5 3 - 20
	GF	11.5 4 - 31	8.5 0 - 19	15.5 0 - 20	5.5 3 - 12	10.5 0 - 18	9 0 - 28	11 5 - 19	8.5 5 - 33
	IM	10.5 4 - 17	10 4 - 28	28 9 - 35	11.5 9 - 14	12 8 - 16	10 0 - 24	5.5 5 - 18	10.5 5 - 30
	IF	7 0 - 14	1 0 - 6	0 0 - 24	3 2 - 13	1.5 0 - 3	0 0 - 26	3 0 - 16	0 0 - 9
Grooming the chin	GM	0 0 - 5	0 0 - 2	1 0 - 4	1 0 - 7	0 0 - 1	0.5 0 - 2	1 0 - 6	1 0 - 6
	GF	1 0 - 5	0 0 - 3	0 0 - 12	0.5 0 - 1	1 0 - 2	0 0 - 2	1 0 - 7	1 0 - 4
	IM	2.5 2 - 3	2 0 - 5	6 0 - 10	2 1 - 3	0 0 - 10	3 0 - 6	1 0 - 2	1.5 0 - 3
	IF	0 0 - 3	0 0 - 0	0 0 - 3	0 0 - 4	0 0 - 0	0 0 - 1	0 0 - 3	0 0 - 0

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Grooming the mid-ventral gland	GM	0.5 0 - 4	1 0 - 3	1 0 - 6	1 0 - 2	3 1 - 5	3 0 - 7	1 0 - 6	2 0 - 3
	GF	1.5 0 - 9	0.5 0 - 2	1.5 0 - 3	1 0 - 1	0 0 - 1	1 0 - 7	1 0 - 5	1 0 - 3
	IM	0 0 - 0	0 0 - 0	0 0 - 2	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 2	0 0 - 2
	IF	0 0 - 3	0 0 - 0	0 0 - 0	0 0 - 2	0 0 - 0	0 0 - 0	0 0 - 1	0 0 - 0
Grooming the genitalia	GM	5 0 - 34	3 0 - 12	10 2 - 29	9 1 - 15	9 1 - 17	5.5 0 - 22	5.5 2 - 53	7.5 0 - 22
	GF	9 0 - 32	6 0 - 10	15.5 0 - 23	6 2 - 16	9 0 - 18	9 0 - 37	7.5 1 - 18	6 1 - 37
	IM	3 1 - 5	0 0 - 0	0 0 - 8	5 1 - 9	0 0 - 1	0 0 - 1	2 0 - 2	0 0 - 3
	IF	0 0 - 7	0 0 - 1	0 0 - 2	0 0 - 1	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Self-grooming	GM	7 1 - 11	6.5 4 - 15	5.5 0 - 14	6.5 3 - 10	6 5 - 6	6 2 - 29	5 0 - 9	8 0 - 20
	GF	6 1 - 15	4.5 0 - 12	6.5 2 - 56	5.5 3 - 9	8.5 4 - 11	7 0 - 16	8 4 - 20	8 1 - 17
	IM	26.5 0 - 53	22 19 - 33	106 64 - 110	31 12 - 50	30 30 - 55	28 12 - 36	23.5 1 - 132	43 18 - 104
	IF	49 4 - 112	7 3 - 85	4 1 - 67	21 0 - 67	30 22 - 53	6 0 - 38	12 7 - 62	12.5 4 - 29
Self-grooming the genitalia	GM	0 0 - 1	0 0 - 1	0 0 - 2	0 0 - 1	0 0 - 0	0 0 - 3	0 0 - 4	0 0 - 7
	GF	0 0 - 0	0 0 - 3	0 0 - 1	0 0 - 1	0 0 - 4	0 0 - 0	0 0 - 0	0 0 - 3
	IM	0 0 - 0	0 0 - 0	0 0 - 1	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 2	0 0 - 3
	IF	0 0 - 0	0 0 - 1	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 2	0 0 - 1	0 0 - 2

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Approaching	GM	13 8 - 19	18.5 17 - 23	24 13 - 40	18.5 9 - 24	15.5 2 - 21	23.5 11 - 36	17 6 - 37	22.5 9 - 43
	GF	14.5 11 - 26	14.5 7 - 22	27 12 - 42	16 6 - 23	24.5 14 - 27	26 7 - 50	18.5 16 - 37	28.5 0 - 42
	IM	18.5 16 - 21	8 5 - 16	49 20 - 71	17 16 - 18	17 13 - 31	22 12 - 24	20 8 - 56	21.5 14 - 55
	IF	22 9 - 32	7 0 - 14	18 2 - 79	15 3 - 23	26 8 - 34	5 1 - 64	9 6 - 37	12 2 - 43
Nosing	GM	9.5 5 - 12	2.5 1 - 9	7.5 0 - 53	11 2 - 17	7.5 1 - 10	7 1 - 16	18 7 - 26	13.5 9 - 23
	GF	8 6 - 13	6.5 2 - 20	6.5 2 - 15	7.5 5 - 13	6 4 - 16	9 1 - 16	11.5 7 - 24	12.5 5 - 27
	IM	10.5 4 - 17	10 4 - 28	28 9 - 35	11.5 9 - 14	12 8 - 16	10 0 - 24	5.5 5 - 18	10.5 5 - 30
	IF	7 0 - 14	1 0 - 6	0 0 - 24	3 2 - 13	1.5 0 - 3	0 0 - 26	3 0 - 16	0 0 - 9

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Sniffing	GM	18 2 - 33	29.5 14 - 47	27.5 6 - 85	13.5 0 - 30	20 15 - 24	22.5 8 - 28	20 2 - 39	39 13 - 84
	GF	24.5 0 - 29	18.5 13 - 36	30.5 2 - 87	10 0 - 43	29.5 16 - 33	27.5 0 - 72	27.5 1 - 48	26 11 - 56
	IM	26.5 0 - 53	22 19 - 33	106 64 - 110	31 12 - 50	30 30 - 55	28 12 - 36	23.5 1 - 132	43 18 - 104
	IF	49 4 - 112	7 3 - 85	4 1 - 67	21 0 - 67	30 22 - 53	6 0 - 38	12 7 - 62	12.5 4 - 29
Mounting	GM	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 20	0 0 - 2	0 0 - 0
	GF	0 0 - 2	0 0 - 2	0 0 - 5	0 0 - 0	0 0 - 4	0 0 - 0	0 0 - 0	0 0 - 4
	IM	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 2	0 0 - 0
	IF	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Foot-stomping	GM	0 0 - 1	0 0 - 0	0 0 - 24	0 0 - 9	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0
	GF	0 0 - 4	0 0 - 4	0 0 - 19	0 0 - 0	0 0 - 2	0 0 - 11	0 0 - 0	0 0 - 9
	IM	0 0 - 0	0 0 - 13	0 0 - 0	1.5 0 - 3	0 0 - 0	0 0 - 1	0 0 - 0	0.5 0 - 7
	IF	0 0 - 0	0 0 - 0	0 0 - 5	4 0 - 7	0 0 - 5	0 0 - 6	0 0 - 2	0 0 - 7
Skimming	GM	0 0 - 1	0 0 - 0	0 0 - 0	0 0 - 8	0 0 - 0	0 0 - 0	0 0 - 23	0 0 - 0
	GF	0 0 - 2	0 0 - 0	0 0 - 0	0 0 - 2	0 0 - 0	0 0 - 0	0 0 - 1	0 0 - 0
	IM	0.5 0 - 1	0 0 - 1	0 0 - 0	0 0 - 0	0 0 - 1	0 0 - 4	0 0 - 11	0 0 - 8
	IF	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 3	0 0 - 0	0 0 - 9

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Digging	GM	23 1 - 42	2 0 - 59	29 1 - 90	26 15 - 51	52 8 - 77	60.5 4 - 106	37 11 - 61	25.5 1 - 67
	GF	28.5 1 - 47	41.5 0 - 58	20 0 - 64	53 2 - 74	63.5 38 - 70	30.5 1 - 52	31 7 - 48	18.5 2 - 60
	IM	16.5 8 - 25	2 0 - 16	5 0 - 9	13 6 - 20	11 0 - 12	34 0 - 42	7 0 - 33	16 1 - 32
	IF	0 0 - 20	2.5 0 - 11	0 0 - 10	2 0 - 4	6 4 - 9	2 0 - 31	1.5 0 - 10	0.5 0 - 9
Boxing	GM	0 0 - 0	0 0 - 0	0 0 - 1	0 0 - 0	0 0 - 0	0 0 - 1	0 0 - 1	0 0 - 2
	GF	0 0 - 4	0 0 - 1	0 0 - 19	0 0 - 4	0 0 - 1	0 0 - 19	0 0 - 1	0.5 0 - 13
	IM	0 0 - 0	0 0 - 1	0 0 - 3	0 0 - 0	0 0 - 1	0 0 - 3	1 1 - 3	0 0 - 0
	IF	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 0	0 0 - 3	0 0 - 0	0 0 - 9

Behavior pattern	Group	Home 1	Home 2	Home 3	Other 1	Other 2	Other 3	Neutral 1	Neutral 2
Hipping	GM	0 0 - 2	3 0 - 27	0 0 - 0	0 0 - 3	0 0 - 0	0 0 - 12	0 0 - 0	0 0 - 4
	GF	0 0 - 7	0 0 - 4	1 0 - 50	0 0 - 12	0 0 - 4	0 0 - 34	0 0 - 0	0 0 - 21
	IM	0 0 - 0	0 0 - 3	0 0 - 4	2.5 0 - 5	5 0 - 6	0 0 - 0	1 0 - 36	1.5 0 - 3
	IF	5 0 - 25	0 0 - 2	1 0 - 4	0 0 - 2	2 0 - 6	0 0 - 28	0.5 0 - 34	0 0 - 37
Defense	GM	0 0 - 3	0 0 - 0	0 0 - 31	0 0 - 4	0 0 - 63	0 0 - 4	0 0 - 0	0 0 - 2
	GF	0 0 - 27	0 0 - 4	0 0 - 37	0 0 - 0	0 0 - 1	0.5 0 - 20	0 0 - 0	0 0 - 61
	IM	0 0 - 0	7 0 - 17	0 0 - 0	0 0 - 0	1 0 - 10	0 0 - 6	0.5 0 - 68	0 0 - 8
	IF	0 0 - 10	17.5 0 - 46	0 0 - 77	12 0 - 71	1.5 0 - 9	7 0 - 87	3 0 - 44	3 0 - 61