学位申請論文

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論文内容の要旨

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（論文題目） Studies on the avoidance and regulatory mechanisms among individuals of a troop of Japanese monkeys,
(Part I, II)
（ニホンザルの個体間の回避および調整機構の研究）

（論文内容の要旨）

主論文2編は、宮崎県幸島のニホンザルを対象にしておこなった社会的相互交渉の分析である。ただし従来の研究とは異なり、個体追跡法によって個体を中心とした社会交渉の量的な把握をおこない、社会構造そのものの理解に新しい視点を確立しようとしたものである。

第1部は、人の影響の少ない森林の中で特定の個体を追跡し、その間にこの個体と群れの個体間に交される個体間交渉を分析した。被追跡個体の近傍3 m以内の他個体が接近した場合に見られる諸種の社会的行動を克明に記載し、この個体が他の特定の1個体との間にどのような出会いを、10時間に平均何回おこなうかというかたちで資料をまとめた。その結果、おとなのメスが自分の子供と相互交渉をもつ頻度は10時間中35回という値を示すが、おとなのメス間、おとなのオス間、オス・メス間の特定2個

体間の平均的交渉頻度は、２回内外にすぎない。さらにこれらの出会いを追従、毛づくろい、音声の応酬、防御的および攻撃的な交渉などの各パターン別に見ると、特定２個体間の特定の交渉は、それぞれ１０時間に0,2回以下という非常に低い値しか得られないことが明らかになった。これは４日に１度程度という低い頻度である。また個体間の交渉の内容については、従来重視されてきた親和的交渉以上に、回避あるいは排他的交渉の出現頻度が高いことが示されている。

申請者は、上記の分析に加えて、被追跡個体の近傍における個体の分布様式や個体密度の算定をおこない、個体間の擦擦を回避する機構として個体の密度が低く保たれていること、これが上記の低頻度の個体間交渉の基盤になっていることを示した。

申請者は上記のような低頻度の交渉では、個体関係の網目が社会関係の網目を保証しえないとして従来のソシオメトリーによる解析法を批判し、さらにニホンザルにおける個体相互間の回避機構の重要性を指摘した。なお、個体は相互に避けあいながら、視覚あるいは遠距離の音声伝達によってゆるやかな連携を保っていると推測している。

第２部は、第１部の結論となった近接回避の傾向を乗り越える必要のある個体間交渉、すなわち身体接触を前提とした毛づくろいが達成されるまでの過程を解析したものである。いま個体Ａ、Ｂが母子でないとすると、ＡがＢを毛づくろいしようとすると、両者間に介在している回避機構を乗り越えてＡはその意図を的確にＢに伝えなければならない。申請者はそのための複雑な記号行動が発達していることを見いだした。まず自らの接近を相手Ｂに知らせ、さらに接近して毛づくろいをしてよいか否かを確認する。それに対してＢは多くの場合それに応ずる意図のある行動を示す。Ａの行動の主要なものは音声であり、申請者はその数種を記載し分析している。とくに〃毛づくろいをしてよいか〃という内容をもつ発声には変異が多く、

流行的現象や群れによる違いが認められた。また申請者は、これらの行動を意図的行動として捉え、接近した個体間でかわされるこの種の記号が、コミュニケーションシステムの発達を考える上でとくに重要であることを強調している。

参考論文3篇中第2篇は、主論文第1部の要約で、第5回国際霊長類学会で発表したものである。第1篇は、異常に大きなサイズをもつ高崎山の群れを対象としてメスの順位的秩序の限界を求めようととしたもの、第3篇は、青島の群れでおこなったメスの順位形成と変動の過程を分析したもので、ともに群れの統合原理を模索しようとしたものである。

主論文

Studies on the avoidance and regulatory mechanisms among individuals of a troop of Japanese monkeys.

Part I. Intra-troop spacing mechanism of the wild Japanese monkeys of the Koshima troop.

Part II. Signals found in the grooming interactions of wild Japanese monkeys of the Koshima troop.

INTRA-TROOP SPACING MECHANISM OF THE WILD JAPANESE MONKEYS OF THE KOSHIMA TROOP

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ABSTRACT

The average frequencies of communicative behavior, social behavior and social encounters (inter-individual proximity within 3 meters) per hour for a monkey were obtained in their natural habitat by tracing several adult males and females of a Japanese monkey troop living in the Koshima islet. The spatial distribution patterns and the density of troop members within the expanse of the troop at any moment were investigated by tracing several adult females. Frequency distributions of the monkeys found within 5 and 10 meters were compared with a Poisson distribution. The frequencies of social encounters and of social interactions of Japanese monkeys were distinctly low, except between mothers and their offspring. The density of monkeys within the expanse of the troop at any moment was very low. Both aggressive behavior and inter-individual proximity (within 3 meters) were distinctly low when monkeys were foraging natural food. An avoiding mechanism among troop members plays an important role in maintaining the social structure of these Japanese monkeys. This mechanism works in two ways: each individual does not approach others too closely; the density of monkeys within the expanse of the troop is low at all times.

INTRODUCTION

Studies of social structure among Japanese monkeys have, up to now, been concerned mainly (with) such social mechanisms for maintaining troop integration as the dominance hierarchy among troop members (ITANI 1954, KAWAI 1958 I, II), kinship relations (KAWAMURA 1958, KOYAMA 1967) and class organization (i.e. central and peripheral members within the troop (ITANI 1954)). These studies were conducted on the assumption that members of a troop were spaced according to a clumped distribution pattern. However, further analysis of this clumping mechanism of the troop members has been neglected. Though Japanese monkeys as a whole have a clumped distribution pattern, it is difficult to say whether they have a clumped distribution within the troop or whether they are randomly or evenly distributed therein.

Using two methods, the author tried to analyse the clumping mechanism of the Japanese monkeys. One method was to investigate the frequencies of social interactions and the situations in which they occurred; the other was to analyse the spatial distribution pattern of the monkeys within a troop.

Interactions among troop members consisted of those which enhance cohesion of troop members and others which cause the dispersion of troop members. These two types of interactions were investigated by recording and analysing all the interactions among troop members. Several adult males and females were individually traced and observed. The situations pertaining to the interactions fall into several categories. The frequency of each category of interactions and the rate of each such frequency to all the interactions were obtained.

On the other hand, tendencies of troop members towards clumping or dispersion were analysed through the study of spatial distribution patterns of troop members. Finally, the relation between the frequencies of social interactions and the density of individuals, as well as the spatial distribution

The study periods for the observations of contexts and frequencies of interactions were August and September, 1970, and the same two months in 1971. The study period for the density and spatial distribution patterns was November, 1971. Because the monkeys live on an islet, few tourists come to see this troop, as compared with other provisioned troops of Japanese monkeys.

Observations were made in the forest of the islet by feeding the monkeys with wheat grains, when monkeys were forced to stay in the neighborhood of the feeding area by the small amount of artificial food.

Scattered on a flat place (14 m x 9.5 m) in the forest about every hour and a half were 2.5 kgs. of wheat grains. Most of the monkeys stopped eating and left the feeding area within 10 or 15 minutes after the wheat grains were scattered. But, when wheat grains were scattered, some monkeys stayed in the feeding area much longer; the leader male, the second male, the most dominant female, the second female and their offspring occupied considerably larger areas than others and stayed there much longer.

Method 1. In order to obtain the records of the frequencies of encounters and interactions among individuals, several individuals were traced and observed, one individual during each tracing period. They were observed when they had departed from the feeding area after all the artificial food were consumed. Cases of inter-individual approach within 3 meters between the traced individuals and others were recorded. Thus, proximity within 3 meters as a whole will be called "encounter" in this report. Positive interactions such as vocalization and threat were recorded even if they were emitted from a distance greater than 3 meters. Interactions among individuals fall into several categories. Among them, passing by, sitting and following are merely proximity within 3 meters

without positive interactions between traced individuals and others. Positive interactions were recorded between traced individuals and others, both for distance less than 3 meters and more than 3 meters. However, most of the positive interactions were observed when the participants were within 3 meters of each other. Tracing observations were continued for about one hour from the time the monkeys departed from the feeding area after consuming the small amount of artificial food until they were again fed with wheat grains in the feeding area. Thus, tracing and recording were repeated for each individual and about 10 hours of recordings for each were obtained. The records of the traced individuals — 7 adult females and 2 adult males — and the length of time of their tracing are shown in Table 2.

During the course of the tracing observation, traced individuals spent more than half of their time in moving and foraging for natural food, being away from the feeding area. Sometimes they spent quite a long time near the feeding area, engaged in such activity as grooming the other members of the troop. Tracing observations were made in the neighborhood of the feeding area from about 9 A.M. until about 3:30 P.M. . Monkeys were fed wheat grains 3 to 4 times a day. At about 3 or 4 P.M., the troop moved away from the feeding area and wandered in its natural nomadic manner. The author considers that the state of the troop when tracing observations were made in the neighborhood of the feeding area represents its state when staying or resting in its natural habitat. Hereafter this state of the troop will be called "stationary state of the troop". The term "the nomad state of the troop" or "moving and foraging state of the troop" will be used when the troop moved around in its natural habitat, foraging for natural food.

Method 2 - A. Because of continuous movement, it was difficult to determine the outer range of the troop at any moment.

Thus, it was also difficult to estimate the density of the individuals of the troop by taking quadrat randomly (quadrat method). So that the density and the distribution patterns of monkeys might be studied, the monkeys were traced and the numbers of individuals that appeared in the 20- and 10- meter diameter circles centered by the traced individuals were counted every 10 minutes. They were traced and observed for about one hour from the time they departed from the feeding area, after consuming a small amount of artificial food, until they were fed again, just in the same way as in the study of the frequencies of interactions. Individuals that appeared in the circles with 20-meter diameters were checked. The distances between the traced individuals and those appearing in the ~~circle with~~ 20-meter diameter circles were measured by eye. Recordings in such circles were conducted 30 times for each of the traced individuals, Imo and Sasa (females of ordinary rank), or a total of 60 times. From these data, numbers of individuals that appeared in each circles with 20- and 10-meter diameters were obtained. Frequency distribution patterns of the numbers of individuals appearing in each such circle were obtained. From this frequency distribution, the spatial distribution patterns of the troop can be known. For example, if monkeys were randomly distributed, the frequency distribution should approximate a Poisson distribution.[2]

The density of the individuals and the range of troop expansion were calculated from the data obtained by the above method; the sum of the number of individuals that appeared in

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[2] If the variance equates mean ($S^2/\bar{x} = 1$), the distribution pattern indicates a Poisson distribution. If variance exceeds mean ($S^2/\bar{x} > 1$), the distribution pattern indicates a clumped distribution pattern. If variance is smaller than the mean ($S^2/\bar{x} < 1$), the distribution pattern indicates an even distribution pattern.

each of the circle is divided by the sum of the area of circles.

One of the problems in the quadrat method that accompanied the tracing of individuals is the effect of the traced individuals on the other monkeys that appear in the circles centered by the former.[3] If individuals are randomly distributed, the traced individual does not affect the distribution pattern of individuals. If the monkeys have an even distribution pattern, the traced individual may affect the number of involved individuals in the circle so as to make them disperse from the traced individual. Accordingly, the traced individuals do not change the tendency of the distribution pattern towards random or even distribution. The state of the troop in the above distribution pattern study corresponds with the state of the troop in the study of frequencies of interactions among troop members — the stationary state of the troop.

Method 2 - B. Monkeys of the troop followed their natural nomad (moving and foraging) after about 3 P.M. . In the nomad state of the troop, monkeys were traced and observed in the same manner as in the stationary state (Method 2 - A). Monkeys that appeared in the circles with 20-meter diameters were checked every 10 minutes. The distances between the traced individuals and those appearing in the circles were measured by eye. The recording was done 20 times for each of the three females of ordinary rank: Imo, Sasa and Nashi. Total recording times were 60. Frequency distribution patterns were analysed in the same manner as in Method 2 - A.

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(3) Since the effect of the social status of the traced individuals was expected, females of ordinary rank were chosen for the traced individuals so as to minimize the effect.

Method 3. A certain length of inter-individual distance seemed necessary to put them at ease. This idea was suggested by two facts: (1) avoiding behavior was observed among monkeys at inter-individual approach, (2) body contact between monkeys rarely occurred except between mothers and their offspring, though a few cases of grooming were observed among non-blood-related individuals. In order to study the minimum distance in which monkeys can be at ease, the distance between each such individual and the one nearest to it was measured in such places as the feeding area, where gathering of monkeys was observed.

Method 4. Up to now, the studies of social structure of the Japanese monkeys have been conducted mainly in feeding areas. However, the author's study was conducted in much more natural conditions. A sharp contrast was observed between the frequency of aggressive interactions observed in the feeding area and in the natural habitat. In order to obtain the data of aggressive interactions in the feeding area, a study was conducted in a 14 m x 9.5 m area when monkeys were fed wheat grains. Four adult females, Zai, Zabon, Aome, Nashi and 2 adult males, Nomi and Ei, were traced and observed for 344 and 453 minutes respectively when they were fed the wheat grains. The frequencies and contexts of aggressive interactions among the traced individuals and the others were recorded.

RESULTS

A. The frequencies and situations of encounters among individuals

In order to obtain the frequency and situations of interactions, 6 adult females and 2 adult males were traced and observed (Method 1). The time duration of tracing observations is shown in Table 2. Recordings of the interactions of adult females and of adult males were obtained for 3797 and 1200 minutes respectively (Table 3, Table 4).

Frequencies of interactions observed were changed to frequencies per 10 hours. The frequencies per 10 hours for each class (adult males, adult females, young males, young females and offspring of traced individuals) were then divided by the number of constituent members of the class.[4] Thus, frequencies of interactions between the members of any pair were obtained (Table 5).

The total frequencies of interactions are the frequecies of encounters (proximity within 3 meters) between members of any pair in this table. While the frequencies of encounters between mothers and their offspring are extremely high — 35.5 times per 10 hours — only about 2 encounters per 10 hours were observed between members of any other pair, regardless of the combinations of the classes. From this calculation, it is clear that, except for a mother and her offspring, any two particular individuals meet only one time in 5 hours. The fact that the frequencies of encounters for different combinations of classes were nearly equal - with two exceptions - suggests that these equal frequencies of encounters were caused by random encounters of troop members in the expanse of troop dispersion. One exception involves interactions between adult females and young females for which 0.98 encounters per 10 hours were observed. The other exception involves those between adult females and young males for which only 0.48 encounters per 10 hours were observed. The latter frequency was 1/4 of that of other class combinations. If the assumption is adopted, that 2 encounters were those of random frequency, the low frequency of encounters between adult females and young males was caused by their avoiding behavior, that is, they avoid

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[4] The average number of offspring of seven traced adult females, 30/7, is used as the number of "offspring" for calculation

each other so as not to approach within 3 meters. In the tracing of adult males, 2.98 encounters between adult males and adult females were observed. This frequency of encounters was higher than that among the same combination of classes obtained in a different tracing observation, the tracing of adult females. The high frequency in the tracing of adult males is explained as follows. The traced adult males had frequent encounters and such specially friendly relationships as frequent grooming with two adult females, one for each of them. These females were not involved with the traced adult females. Nomi's favorite was Goma, a 5-year old female, and Ei's favorite was Maki, a 5-year old female. Both Goma and Maki gave their first birth in the year.

Looking at the situations of interactions, mere proximity, such as passing by and sitting, accounts for half or more than half of the total interactions. For each category of such positive interactions[5] as grooming and aggression, the frequency observed was well below 0.2 times per 10 hours. If the Japanese monkeys are active for 12 hours a day, the frequency of each interaction between two particular individuals is considerably less than once in 4 days.

In order to examine the situations of encounters, the

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(5) When more than one interaction took place in a series, the most significant one among them is chosen as representative. One example is "grooming"; grooming interaction sometimes involved "sitting" and "vocalization" that induced grooming. When a third individual intervenes in the aggressive interaction of two other individuals, the interaction of the third individual with the other two is put into the category of cooperative interaction. One such case is a mother's intervening interaction in the aggressive interaction between her child and others.

rate of the frequency of each category of interaction to that of total interactions (encounters) among each combination of classes is calculated (Fig. 1). Mere proximity within ? meters, passing and sitting, showed the highest rate among all of the interactions, though the interactions depend on the distance given as a criterion of encounter, 3 meters in this report. The rate of ~~the passing and~~ sitting between mothers and their offspring was higher than in any other combination of classes. Further, the rate of sitting between mothers and their offspring exceeded that of passing and it may indicate that sitting must be a positive interaction among them. The high rate of grooming interaction was obtained between mothers and their offspring. The rate of moving away or avoiding interaction at inter-individual approach was high both among adult females and among adult males. Aggressive interaction accounted for 2 to 9 % of the encounters.

Three kinds of interactions, passing, sitting and following, were considered to be the merely proximity within 3 meters. Therefore, other interactions except for these three were called to be "positive interactions". Positive interactions were selected from the total interactions shown in Table 5. The ratio of each interaction to the total positive interactions was calculated (Table 6). Positive interactions accounted for 17 to 50 % of the total interactions. The highest rate was 50 % among adult males, and the lowest was 17 % between adult females and young males. The rate of positive interaction between mothers and their offspring was not so high. If following is included as a "positive" interaction, the rate of the positive interaction among them will reach 50 %. Positive interactions can fall into three categories: (1) friendly interactions (grooming, co-feeding, vocalization, cooperation in aggressive interaction, mounting): (2) avoiding interaction (taking a circuitous way, moving away, defensive expression),

and (3) aggressive interaction. When the ratio of each of these three categories of interactions to the total positive interactions is examined, the sum of the frequencies of avoiding interactions and aggressive interactions exceeds that of friendly interactions, except for the class of mothers and their offspring.

In summary, the frequency of inter-individual proximity between these Japanese monkeys is very low, except between mothers and their offspring. Positive interactions accounted for less than 50 % of the total interactions (encounters). Further, the sum of the frequencies of avoiding interactions and aggressive interactions exceeded that of friendly interactions, except for the class of mothers and their offspring.

B. Aggressive interactions and feeding behavior

The contexts of the total 82 aggressive interactions, which were observed during the course of the tracing observation of adult females (for 3797 minutes) and adult males (for 1200 minutes) (Table 3, Table 4), are shown in (Table 7). Twelve aggressive interactions were observed when body contact or inter-individual approach (following, proximity, friendly proximity, body contact) took place. Forty aggressions had such social meaning as related dominance rank or control attack by males (competition to groom dominant individuals, competition to be mounted by dominant males, compensation attack to the third individual when the aggressor was attacked by another individual, cooperation in aggressive interactions). Thirteen aggressive interactions were observed when one of the participants was foraging for natural food. Five aggressive interactions were observed after the monkey that was being aggressed had emitted vocal sounds. Eight aggressions were observed in other situations. Each of the 13 aggressive interactions at the time of foraging occurred between traced

individuals and young individuals. Thus, aggressive interaction was not observed among adult individuals when they were foraging.

Aggressive interactions which appeared when they were foraging for natural food and which were observed during the course of the tracing observation have already been examined. Examined here is the inter-individual approach without aggression when monkeys were foraging for natural food and were observed during the course of the tracing observation (Table 3). During this tracing observation traced individuals were frequently observed when foraging (Method 1). However, cases of proximity within 3 meters without aggression during such foraging were not observed at all among non-blood-related individuals, though a small number of cases of proximity were observed between mothers and their offspring (Table 3). Only 3 cases of proximity among non-blood-related individuals were observed, when they were drinking water. Proximity cases without aggression between mothers and their offspring, observed during the course of the tracing of adult females for 3797 minutes, were classified into 6 categories according to the kinds of food and also to the places where they foraged, on the ground or in the trees (Table 8). During the course of the tracing of adult males for 1200 minutes, cases of proximity within 3 meters were not observed at all during foraging activity. Only 2 cases of proximity were observed when traced adult males were drinking water.

In summary, cases of proximity, both with and without aggressive interactions, when they were foraging for natural food (Tables 7 and 8), were not observed among adult individuals. Cases of proximity without aggression were not observed among non-blood-related individuals. Only 6 cases of proximity with aggressive interactions were observed between adult females and young females and only 4 such cases were observed between

adult females and young males; the frequencies were changed to 0.025 and 0.021 times per 10 hours.

In summary, when they were foraging for natural food, the frequency of proximity within 3 meters was extremely low, and such cases of proximity among adult individuals were not observed at all during the course of the tracing observation. Thus, it is reasonable to say that the frequency of aggressive interactions is very low when they are foraging.

The results obtained in their natural habitat are in sharp contrast to the impression that the frequency of aggressive interactions among Japanese monkeys is very high in feeding areas. In order to show the difference in aggressive interactions between the results obtained in the monkeys' natural habitat and in a feeding area, aggressive interactions were observed in the feeding area ($14^{m}_{\wedge}$ x 9.5 m) by tracing several monkeys (Method 4). Scattered in the feeding area every 1 and half hours were 2.5 kilograms of wheat grains. Most of the wheat grains were consumed in 10 to 15 minutes after being scattered. Four adult females (Zai, Zabon, Aome and Nashi) and 2 adult males (Nomi and Ei) were repeatedly traced individually and were observed for a total of 344 and 453 minutes respectively (Table 9). The frequencies are changed to the frequencies per 10 hours and were compared with the frequencies of aggressive interactions in the monkeys' natural habitat that were shown in Table 5 (Table 10). Aggressive interactions in the feeding area were observed 76 times per 100 hours during the course of tracing adult females and 183 times per 10 hours when tracing adult males. However, 6.3 of the former and 11.0 of the latter were observed in their natural habitat (in the neighborhood of the feeding area). These represented only 1/12 and 1/17, respectively, of the total aggression in the feeding area. The high frequencies of aggressive interactions in the feeding area were caused by the overcrowding of monkeys

in the feeing area, though the feeding area was very small as compared with usual feeding areas.

C. The spatial distribution patterns of monkeys in the troop

1. The troop staying in the neighborhood of the feeding area

Now, let us consider the other method by which the clumping of the troop was investigated i.e., that of the spatial distribution patterns.

The frequencies of inter-individual encounters are considered to be correlated with the density and distribution patterns of individuals. As the author intended to obtain the distribution patterns and density relevant to the frequencies of encounters, the number of individuals was investigated in the area of expansion of members of the troop at any moment, and, generally, not investigated in the home range area. The details of the method are as follows (Method 2 - A). Two adult females, Imo and Sasa, were traced and the numbers of additional individuals that appeared in the circles centered by the traced individual were counted every 10 minutes when the troop was staying in the neighborhood of the feeding area. The diameters of the circles at each counting were 20 and 10 meters respectively. Data were obtained 60 times for each circle (Table 11). The frequency distributions of the number of individuals appearing in each circle were obtained when the troop was staying in the neighborhood of the feeding area (Table 11). The frequency distribution of the numbers of all the other individuals appearing in the circle with a 20-meter diameter, except for babies and offspring of traced individuals, is shown (Table 11, Fig. 2). The Poisson distribution, whose total number of individuals is equated with the observed total number of individuals that appeared in the circles, is also indicated in Fig. 3. When compared with the Poisson distribution, the

observed distribution pattern indicates the clumped distribution. The ratio of variance to mean ($S^2/\bar{x}$) was 5.38. The tendency towards clumping was expected among mothers and their offspring, because of the high frequency of encounters among them. Therefore, adult females were selected from the above data (Table 11, Fig. 3 - a). A slight tendency towards clumping of adult females was observed in the 20-meter diameter circles; the ratio of variance to mean ($S^2/\bar{x}$) was 2.51. The frequency distribution of the numbers of adult females appearing in the circles with 10-meter diameters was likewise obtained (Table 11, Fig. 3 - b). The distribution pattern approximated a Poisson distribution; the ratio of variance to mean ($S^2/\bar{x}$) was 0.97. Thus, adult females were randomly distributed in the 10-meter diameter circles. Further, the total number of individuals appearing in such circles was 23. This is nearly 1/4 (the ratio of areas of the circles) of the number of individuals, 102, that appeared in the 20-meter diameter circles.

In summary, the adult females were randomly distributed in the 10-meter diameter circles, whereas they had a slightly clumped distribution pattern in the 20-meter diameter circles. The random distribution pattern of adult females in the 10-meter diameter circles agrees with the suposition that nearly equal frequencies of encounters (proximity within 3 meters) for different combinations of classes were caused by random encounters of troop members in the expanse of troop dispersion.

In order to grasp the features of concentration of individuals, the changes in the density of individuals in correlation with the changes of distance from an individual were examined. In the tracing observation in which distribution patterns of individuals were investigated (Method 2 - A), the distances between the traced individual and individuals appearing in the circles centered by the traced individuals, were measured by eye. All of these data (Method 2 - A) have been examined.

In order to obtain changes of density in correlation with changes of distance from an individual, numbers of adult females that appeared in the doughnut-areas of concentric circles centered by the traced individuals (Table 12), were divided by the areas (Fig. 4). Adult females more frequenty stayed within the distance of 4 to 6 meters from the traced individuals. Adult females rarely approached within 2 meters of the traced individuals (Table 12). However, the density within 2 meters from the traced individuals, indicated as zero (Fig. 4), is a false figure because of insufficient data. The numbers of individuals, (that ~~who~~) appeared in the doughnut-areas practically decreased to zero (Table 12) in accordance with the decrease in distance when the data were insufficient. Thus, the density was calculated as zero in spite of the decrease in the doughnuts areas (Table 12).

The individuals appearing in the proximity of traced individuals were so few in the above data that it is difficult to know the minimum distance where monkeys can stay at ease. Thus, the distance between individuals nearest to each other was measured in such places as around the feeding area where the gathering of monkeys was observed (Method 3) (Fig. 5). The minimum distance where monkeys could stay at ease was 2 to 3 meters and was never less than 1.5 meters.

2. Moving and foraging state of the troop

The troop moved away from the feeding area and underwent its natural nomad at about 3 or 4 P.M.. In order to investigate the spatial distribution patterns of the monkeys when the troop was moving and foraging in its natural habitat, 3 adult females (Imo, Sasa and Nashi) were traced and numbers of individuals that appeared in the 20- and 10-meter diameter circles centered by the traced individuals were counted (Method 2 - B). These data were obtained 60 times for each circles

(Table 13). Frequency distributions of the numbers of individuals, except for the offspring of traced individuals and babies, that appeared in both circles are indicated in Fig. 6 - a, b together with the Poisson distributions where total numbers are equated with observed total numbers of individuals. Frequency distributions of the numbers of individuals in both of the 20- and 10-meter diameter circles, approximated Poisson distributions. The ratios of variance to mean ($S^2/\bar{x}$) were 1.40 and 1.16 respectively for the 20- and 10-meter diameter circles.

Thus, monkeys, except for the offspring of traced individuals and babies, were randomly distributed in both circles.

The above data showed that monkeys, including both adult and young individuals, were randomly distributed when the troop was moving and foraging, whereas they showed a tendency towards clumping when the troop was staying in the neighborhood of the feeding area.

D. Density of individuals

The frequencies of inter-individual encounters are considered to be correlated with the density of individuals. In this sense, density will be defined as follows; the number of individuals divided by the area of expansion of members of the troop at any moment. Thus, densities of individuals are calculated from the data, already used in section C (Method 2 - A, B). The numbers of individuals appearing in the circles with 20-meter diameter were obtained 60 times for each of the state of the troop — stationary and moving and foraging. Thus, the total numbers of individuals that appeared in the 60 investigation times (Table 14) were divided by the total areas ($\pi \times 10^2$) x 60 m^2 for the stationary state and for the moving and foraging state of the troop (Table 14).

The density of adult females and that of all individuals except for the offspring of the traced individuals and babies were 0.54 and 1.65 individuals per 100 m^2 respectively, when the troop was staying in the neighborhood of the feeding area. When the data of density in the troop's stationary state was obtained, the state of the troop was just the same as its state when the frequencies of inter-individual encounters were obtained. The frequencies of inter-individual encounters were obtained (Method 1) by counting the numbers of individuals that appeared in the circle with 6-meter diameter centered by the traced individuals in the duration of tracing observations. Thus, the distances which were necessary for the monkeys to move to attain the observed frequencies of encounters (Table 5) in the density of individuals calculated above (Table 14), can be roughly calculated. Monkeys are postulated to have moved straight for α meters per an hour. Then, the area which the circle with a 6-meter diameter centered by the traced individual covered, reaches α x 6 m^2 per an hour. The observed frequencies of encounters per an hour are considered to equate the number of individuals that appeared in the swept area (α x 6 x density/m^2). Thus, the distances of movement of monkeys per hour are calculated (Table 14). The distance of movement per hour was 100 m on an average, with not much difference among the different classes, adult males, adult females and young individuals. The results agree with the impression obtained during the course of observations. The calculation of movements of monkeys was conducted on the hypothesis that the frequencies of encounters were caused by the random movements of monkeys in the density of monkeys. And, the fact that the calculated distances of movements roughly agreed with the observed distances, indicates that the hypothesis was reasonable.

The ranges of troop expansion at given moments were

calculated from the data of the densities (Table 14). The ranges of expansion were 53 x 100 m^2 in the stationary and 203 x 100 m^2 in the moving state of the troop. The ranges of expansion in the moving and foraging state were 4 times that in the stationary state of the troop. This result agrees with the impression obtained during the coruse of the observation. Thus, the frequencies of inter-individual encounters when the troop was moving and foraging must have been far less than those obtained during the course of the tracing observation when the troop was staying in the neighborhood of the feeding area. This assumption also agrees with the impression obtained during the course of observation.

Since the frequency of inter-individual proximity within 3 meters was very low when they were foraging natural food, the density of food plants was compared with that of monkeys (Table 15). Station 1 was on the slope facing the sea. Stations 2 and 3 were in the forest. The number of woody plants having more than 4-centimeter diameters at a height of 1.5 meters were counted for 3 species of staple food, tabunoki (Machilus Thunbergii), himeyuzuriha (Daphniphyllum Tejismanni) and inubiwa (Ficus erecta). The number of each of these species per 100 m^2 was twice the number of monkeys in the troop in its moving and foraging state and the amount of these 3 species was 16 times the density of monkeys in stations 2 and 3, though the number of woody plants was much smaller as compared to station 1. In station 1, the sum of these 3 species was 56 times the number of monkeys. The sum amount of these 3 species of woody plants greatly exceeded the density of individuals in the troop's moving and foraging state. Further, one monkey does not occupy two or more trees at a time. The data also indicate that aggressive interactions have very low frequency when the monkeys are foraging for natural food.

DISCUSSION

The frequency of inter-individual proximity within 3 meters between the Japanese monkeys is very low except between mothers and their offspring in their natural habitat. Studies on the social structure of the Japanese monkeys have, up to now, been conducted mainly in feeding areas. In feeding areas, where monkeys get clumped or crowded, frequencies of encounters among them were extremely high. Thus, studies in the feeding areas gave false impression that the unity of the troop was maintained through the frequent interactions among troop members. This impression given by studies in the feeding areas must have had relation to the problems studied up to now, and these problems were based on the clumping of troop members.

The results of this report indicate that the frequencies of inter-individual proximity between the monkeys were very low, except between mothers and their offspring. Furthermore, the frequencies of positive interactions were less than half of the frequencies of proximity, inter-individual approach within 3 meters. Positive interactions can fall into three categories — friendly, avoiding, and aggressive. The sum of the frequencies of avoiding and aggressive interactions exceeded that of friendly interactions, except for the class of mothers and their offspring. Other data indicated that inter-individual proximity within 1.5 meters was rarely observed among non-blood-related individuals, except for grooming.

No behavioral tendency or social mechanism which produces clumping of troop members could be seen. Rather, avoiding behavior was evident. The avoiding mechanism is important in maintaining the social structure of the Japanese monkey troops, while the unity of the troop has been supposed to be maintained

through the frequent interactions among troop members.

On the other hand, the spatial distribution patterns indicate that the monkeys were randomly distributed in the 10-meter diameter circles. This result agreed with the frequencies of inter-individual encounters which were caused through random encounters of individuals in the expanse of troop dispersion. It suggests that the frequencies of inter-individual encounters are dependent on the density of individuals. Thus, low frequencies of such encounters may be due to the low density of the monkeys, if the frequency is random. The ranges of expansion of the troop were 5300 m^2 for the stationary state and 20500 m^2 for the moving state in the Koshima troop which consisted of 110 monkeys. These ranges of expansion of the troop were far broader than usual feeding areas. Accordingly the mechanism of avoiding each other may be based on maintaining a low density of individuals.

Indeed, avoiding behavior was frequently seen by the author when observing the famous provisioned Takasakiyama troops in Oita prefecture, for the 2 months in 1969. Because the population size of the Takasakiyama A troop was extremely large, so many monkeys were crowded in the feeding area. It appears that the avoiding behavior must have worked for the regulation of the troop in high population density.

So far, the importance of avoiding mechanism among Japanese monkeys has been indicated. The next problem is the mechanism of clumping of monkeys as members of the troop. Clumping was appearent among mothers and their offspring. And clumping of monkeys was observed in the 20-meter diameter circles when the troop stayed in the neighborhood of the feeding area. Thus, the monkeys have a tendency towards clumping together when the distance is long and they communicate with long distance vocal and visual communication. Contrariwise, they move randomly when the distance is short and they can have more direct

interactions. When the troop was moving and foraging, clumping was not observed in the circles of either 10 or 20 meter diameters. Thus, they are supposed to have communicated only through vocal communication when they were moving and foraging.

Roughly speaking, there are some correlations between the group sizes and their habitats (STRUHSAKER 1969, CROOK and GARTLAN 1966, KUMMER 1971). The environmental factors which affect group sizes are food resources, predators, sleeping sites, visibility of coordination of group movements, etc. Among these, food resources are considered the most important factor; if the population size of a group is large, more monkeys will come to a certain food resource than its capacity warrants. Now, let us examine this factor in the case of the Japanese monkey. The Japanese monkeys are forest-living monkeys. The population sizes of wild troops are 20 to 100 animals, and group sizes increased to more than 150 animals in provisioned troops. Though the 110-monkey size of the Koshima troop was fairly large, the competition for food resources was not observed, and the density of monkeys within the expanse of the troop remained low. The competition for food resources can be reduced, therefore, by keeping the density of monkeys low and by mainkg the range of expansion of troop members large. The mechanism of maintaining low density of monkeys depended on their spacing behavior, especially that observed when they were feeding on natural food. The author observed that monkeys always uttered contact calls and they moved about in the areas where they could hear the contact calls of other monkeys when they were foraging and moving in the forest of the Koshima. When they failed to hear contact calls of other monkeys, they made the strong characteristic vocal sound, (hogaa. hogaa ....), until they could get responses from other monkeys. Then they moved in the direction of the vocal responses. Thus, the density of monkeys within the expanse of the troop was kept low

and the increased population did not affect the density of monkeys when they were exploiting natural food resources.

Up to now, in order to grasp the mechanism of clumping of troop members, the author has analysed the problem, through the study of spatial distribution patterns of troop members or through the study of the frequencies of inter-individual encounters. This problem has been studies mainly through observing activities which enhance clumping of troop members, such as social behavior, or through observing ~~of~~ social structure which supports the unity of troop members. The results in this report indicated that the unity of the troop is supported by avoiding mechanism of monkeys; avoidance of bodily contact and interactions among troop members.

Next, the frequencies and roles of the social behavior which have been major subjects of studies of Japanese monkeys will be examined in order to see the mechanism of clumping of the members of the troop. Though it is difficult to make a decisive conclusion, an important aspect concerning the frequency of social behavior was obtained. For each category of such positive interactions, such as grooming and aggression, the frequency observed between any pair of monkeys was considerably less than 0.2 times per 10 hours when the troop stayed in the neighborhood of the feeding area. If the monkeys are active for 12 hours a day, the frequency of each interaction between two particular individuals is less than once in 4 days. The density of monkeys when they were moving and foraging was 1/4 of that obtained when they were staying in the neighborhood of the feeding area. Therefore, the frequencies of interactions must have been much less than the frequencies calculated above in their daily activity. Thus, it must be pointed out that social interactions in a short time span do not give insight into the social structure, though there must be some difference in the frequencies of interactions among different pairs of

monkeys. The experiences of interactions must be memorized and kept quite a long time if the interactions are adopted into the social order. Social order must be based on the experiences over quite a long time.

Therefore, the studies on social structure in the feeding areas are misleading. In such areas, monkeys are clumped or crowded, and frequencies of encounters among them are extremely high. In addition, aggressive interactions in the feeding area when they were eating artificial food were at least 12 times that in their natural habitat in the same time unit.

Studies of the aggregation of monkeys up to now have been conducted mainly on the difference of the intensity of bonds between different combinations of components of troop members, age, sex, kinship etc. (MARLER 1968), though some quantitative data of spatial distribution pattern are available (KUMMER 1968). The author analysed quantitatively the intra-troop spatial distribution patterns correlated with densities of individuals. And by this method he examined whether the frequencies of inter-individual encounters or of social interactions are random or not.

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LEGENDS

Fig. 1. Ratio of the frequency of each interaction to that of the total interactions among individuals of each combination of classes (from Table 5). (a) Adult females were traced and observed (b)Adult males were traced and observed.

Fig. 2. Frequency distribution of numbers of individuals that appeared in the circles with 20-meter diameters. (The troop stayed in the neighborhood of the feeding area.)
The solit line indicates observed frequency distirbution of numbers of individuals that appeared in the circles except the offspring of traced individuals. The dotted line indicates Poisson distribution.

Fig. 3. Frequency distribution of adult females appearing in the circles. (The troop stayed in the neighborhood of the feeding area.) (a) The diameter of the circle is 20 meters. (b) The diameter of the circle is 10 meters.
Solid lines indicate the observed frequency distributions of the numbers of adult females that appeared in the circles. Dotted lines indicate Poisson distributions.

Fig. 4. Correlation of distances between monkeys and density of adult females at these distances. (The troop was staying in the neighborhood of the feeding area.) The traced individuals were Imo (solid line) and Sasa (dotted line).

Fig. 5. The smallest inter-individual distances.
The smallest distance was measured in such places as around the feeding area where gathering of monkeys was observed (Method 3). Black bar: smallest distances between adult females, dotted bar: distances between adult females and adult males, blank bar : distances between adult females and young individuals.

Fig. 6. Frequency distribution of numbers of individuals that appeared in the circles except the offspring of the traced individuals. (The troop was moving and foraging.) (a) The diameter of the circle is 20 meters. (b) The diameter of the circle is 10 meters. Solid lines indicate the frequency distributions observed. Dotted lines indicate Poisson distributions.

Table 1. Age/sex composition of the Koshima troop (Sept. 1971).

adult males (more than 6 yrs.)	4	adult females (more than 4 yrs.)	25
young males (1-6 yrs.)	31	young females (1-5 yrs.)	34
infant males (less than 1 yr.)	12	infant females (less than 1 yr.)	4

Five year old females who have not given birth are put into the class of young females. This troop consists of males under 6 years and over 14 years. Thus, 1 to 6-year old males are put in the same category as "young males".

Table 2. Duration of tracing observation.

individual traced		age in years	duration of tracing (minutes)
adult females	Zai	12	600
	Zabon	15	600
	Aome	16	600
	Nashi	14	600
	Sasa	15	449
	Imo	18	540
	Ine	11	408
adult males	Nomi	18	600
	Ei	17	600

Table 3. The frequencies of inter-individual interactions observed when seven adult females were traced.

traced individuals	partners of interactions	passing		sitting		following		grooming		foraging		vocalization		taking circuitous way		moving away		defensive expression		threat		driving away		attack		cooperation		others	
		A**	P**	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P
Zai	Ami*	1	2	1	25		16	11	3		6													1		1		1	
	Azaimi*		1	2	11		3	7	8																				
	Ashi*			1	2		3	1	6																				
	ad.♀	3	4	6	3	2	1	4				2	1		4	8												1	
	ad.♂		2	1	1																								
	young♀	2	11	5	8				4			2	2			1	4		2					2	1				
	young♂	1	4	4	1										2		1												
Zabon	Boke	2	2		42		9	5	10																				
	Bote	1		2	27		7	13	4																				
	Bozu	2		1	25		6	4	15		1		1			1	1			1								
	Boze	1			3																								
	ad.♀	3	7	4	3			1	2				2			4	2												
	ad.♂	1	3	1																									
	young♀	2	6	3	8		2		4				8				1								1				
	young♂	2	2		3																								
Aome	Zarame	1	2	1	11		17	3	4		3		1																
	Zasso			2	7				5																				
	Zakuro	5	1	2	13		4	12	3	1	2		1														1		
	Zashin	1			2		1																			1			
	ad.♀	12	5	1	3		1					1				13	3	3				3	1						
	ad.♂		2															2				1							
	young♀	5	10	2	3						1		1			2	5												
	young♂	5	10	2	6						1						1	1		2									
Nashi	Shiran	1	1	1	20		4	10	1				1													1			
	Shishi	2			17		3	5																					
	Shion	3	5	1	18		5	13	9								2		1							1			
	Shiba	2	2	3	11		2	13	7								1												
	Baku	1	2	4	6		1																	1					
	ad.♀	8	7	7	10			1		1		6	1	1			4												
	ad.♂	2	5	4	1											2		1											
	young♀	4	9	1	14		2								3		5		1	1		3		1					
	young♂	5	6	1	8												2			2									
Sasa	Sachi	1	1	2	5		1	8					2																
	Sasage	1	1	2	13		8	2	2			1	2				1									1			
	Sarume			1	8		2	3	4																				
	Sayuri	2	1	1	11		3		5				5				2			1		1				3			
	Sakaki		1	2	5	2		3	1			2				2													
	ad.♀	2	3	3	6	1	1		3			3	6			7					1	1	2	2					
	ad.♂			3	3											1				1			1						
	young♀	1	1		3								1										1	1					
	young♂		2	1	5																								
Imo	Ira			7	15		12	2	1	1		1	4									6		1					
	Ichyo		3	2	16		11	6	5			1	2				1												
	Itachi	1		4	6		7	3				1																	
	Ikaru	2	2	3	8		2																						
	Isu	1	3	6	6		6	5	4	1		2	2			1	1		1	1						2			
	Ine		1	3	3				1			1					1												
	ad.♀	2	3	4	3			5				4	1			3	1							1					
	ad.♂	2	2	1	1													2				1							
	young♀	2	2	3	7				2						1					1		1		2					
	young♂	1	2														1							2					
Ine	Nemu			2	7		4	7					2			1													
	Neko	1			11		4	2	3																				
	Negi			2	2	1	2	5	5				1			1						1							
	ad.♀	3	9	3	3	1		3	4			2	9			4	2			1									
	ad.♂	1	1	1																									
	young♀	2	3	1	11				1				2				1			1		1		1					
	young♂		2		3												1												
sum	children of traced individuals	33	31	58	356	3	143	143	106	3	12	9	24			6	10		2	4		8		3		10	1	1	
	ad.♀	33	38	28	31	4	3	14	8	1		18	20	1	4	39	12	3		1	1	4	3	3				1	
	ad.♂	6	15	11	6											3		5		1		2	1						
	young♀	18	42	15	53		10		11	2	3		12	1	8	2	14		1	3		5	1	7	2				
	young♂	14	28	9	28						1				2		6	1		4				2					

* Individuals indicated by their names are children of traced individuals.

** A: behavior of traced individuals, P: behavior practiced by the individuals who came close to the traced individuals. Durations of tracing are indicated in Table 2.

Table 4. The frequencies of inter-individual interactions observed when two adult males were traced.

traced individuals	partners of interactions	passing		sitting		following		grooming		foraging		vocalization		taking circuitous way		moving away		defensive expression		threat		driving away		attack		cooperation		others
		A**	P**	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	
Nomi*	ad. ♀	12	13	15	17				14		2		1		2	3	9		2				1	1					
	ad. ♂			5	1			1									1								1			*** Mt.2, Mz.1 ***
	young ♀	8	21	13	19		2		3				4				5			1		4						
	young ♂	8	9	8	17		4		4			1	1		1	1	3											Mt.2, Mz.1
Ei*	ad. ♀	2	8	6	14		1	1	8					1	1		7			2		2				4		
	ad. ♂		1														1											
	young ♀	3	9	5	16		1		1			1		1	1	1	1		2			4	2			1		
	young ♂	2	12	14	14		3		5								4		4	2		1						Mt.1, Pr.1 ***
	sum	35	73	66	98		11	2	35		2	1	7	2	5	4	31		8	5		12	3	1		5		Mt.4, Mz.2 Pr. 1

* Nomi and Ei were traced and observed for 600 minutes each. ** A: behavior of traced individuals, P: behavior practiced by the individuals who came close to the traced individuals. *** Mt: mounting, Mz: mouth to mouth contact, Pr: presenting.

Table 5. Frequencies of inter-individual interactions between two particular individuals per 10 hours.

traced individuals	individuals that had interactions with traced individuals	passing	sitting	following	grooming	foraging	vocalization	cooperation	mounting	circuitous way	moving away	defensive	aggressive	total (encounter)
ad ♀	offspring	2.3	15.3	5.4	9.2	0.6	1.2	0.4			0.6	0.07	0.6	35.5
	ad ♀	0.47	0.39	0.05	0.14	0.01	0.25			0.03	0.34	0.02	0.08	1.77
	ad ♂	0.8	0.7								0.1	0.2	0.2	2.0
	young ♀	0.28	0.32	0.05	0.05	0.02	0.06			0.04	0.07		0.08	0.98
	young ♂	0.21	0.19			0.01				0.01	0.03	0.01	0.03	0.48
ad ♂	ad ♀	0.7	1.04	0.02	0.46	0.04	0.02	0.08		0.08	0.38	0.04	0.12	2.98
	ad ♂	0.2	1.0		0.2				0.3		0.3		0.2	2.3
	young ♀	0.6	0.78	0.04	0.06		0.07			0.03	0.09	0.03	0.16	1.9
	young ♂	0.5	0.85	0.11	0.15		0.03		0.05	0.02	0.13	0.06	0.05	1.98

Number in each cell is mean frequency of interaction between a traced individual and a member of each class for 10 hours i.e. total frequency for each interaction between a traced individual and members of a particular class is divided by the number of constituent members of the class. The total numbers of interactions are frequencies of encounter (proximity within 3 meters).

Table 6. Rate of avoiding interactions in total cases of positive* interactions.

	class combination of interactions	rate of positive interactions in total encounter (%)	ratio to total positive interactions: moving away (%)	aggressive interactions (%)	avoiding** + aggressive interactions (%)
tracing observation of adult females	ad.♀ - offspring	35	5	4	10
	ad.♀ - ad.♀	49	39	9	54
	ad.♀ - ad.♂	24	25	33	100
	ad.♀ - young♀	34	22	25	61
	ad.♀ - young♂	17	38	38	94
tracing observation of adult males	ad.♂ - ad.♀	41	31	10	51
	ad.♂ - ad.♂	50	40	20	60
	ad.♂ - young♀	25	19	39	71
	ad.♂ - young♂	26	28	10	55

* Positive interactions; Three kinds of interactions, passing, sitting and following, were considered to be the mere proximity within 3 meters. Then, other interactions except these three were called to be "positive interactions".

** Avoiding interaction = moving away + taking circuitous way + defensive interactions

Table 7. Situations of aggressive interactions observed during the tracing observations.

traced individuals	aggressor / aggressee	following	proximity	friendly proximity	contact	vocalization	foraging	baby	to groom dominant monkeys	compensation	defensive cooperation	aggressive cooperation	others
adult females	mothers / children	1	2		2		2		6		5	1	
	children / mothers								1		1		
	ad.♀ / ad.♀		1	1				1		3	2	1	2
	ad.♀ / young♀		2			2	6			1	1	1	2
	young♀ / ad.♀		1								1		1
	ad.♂ / ad.♀							1				1	
	ad.♀ / ad.♂										1		
	ad.♀ / young♂						3	1			1	1	
	young♂ / ad.♀						1						
adult males	ad.♂ / ad.♀									1	2	2	1
	ad.♂ / ad.♂							1					
	ad.♂ / young♀		1			2	1		1	2	1		2
	young♀ / ad.♂									2			
	ad.♂ / young♂		1			1			1				
sum		1	8	1	2	5	13	4	9	9	15	7	8

The tracing observations of adult females and adult males were conducted for 3797 and 1200 minutes.

Baby; The monkeys staying close to the crying babies were sometimes attacked by their mothers or adult males.

Table 8. Inter-individual proximity without aggression when monkeys were feeding on natural food.

	approacher		being approached		on trees			on the ground				number of cases
		relation-ships		relation-ships	leaves	nuts	insects	nuts	grass	water	mud	
mothers and children	Ami	son of Zai 1 yr.	Zai		0							2
						0						2
							0					2
	Bozu	son of Zabon 4 yrs.	Zabon					0				1
	Zarame	daughter of Aome, 1 yr.	Aome		0							1
										0		1
											0	1
	Zakuro	daughter of Aome, 4 yrs.	Aome		0							1
	Aome		Zakuro		0							1
	Imo		Ira	son of Imo, 1 yr.					0			1
	Imo		Isu	daughter of Imo 5 yrs.					0			1
non-blood-related individuals	Ichyo	3 yrs.	Aome	20 yrs.						0		1
	Ira	1 yr.	Aome							0		1
	Aome	20 yrs.	Goma	5 yrs.						0		1

The data were obtained during the tracing observations of adult females for 3797 minutes. The circles indicate the kinds of food foraged for in each case of inter-individual proximity. Inter-individual proximity without aggression when monkeys were feeding on natural food were not observed during the tracing observations of adult males for 1200 minutes except for two cases in which monkeys were drinking water.

Table 9 - (1). Aggressive interactions with particular adult females in the feeding area.

situations / combinations	proximity			joining aggressive interactions of others		
ad.♀ - ad.♀	M 84	Df 3	Th 1			Th 4
	Dr 22	At 2	B 4	Dr 2	At 2	
ad.♀ - ad.♂	M 11					
		At 2				B 1
ad.♀ - young ♀	M 6					Th 1
	Dr 2	At 1				
ad.♀ - young ♂	M 11	Df 1				
total	M 112	Df 4	Th 1			Th 5
	Dr 24	At 5	B 4	D 2	At 2	B 1

Durations of observations (minutes): Zai 154, Zabon 75, Aome 27, Nashi 88, total 344 minutes.

M: move, Df: defensive face, Th: threat, Dr: drive, At: attack, B: bite.

Table 9 - (2). Aggressive interactions with particular males in the feeding area.

situations / combinations	proximity	joining aggressive interactions of others	compensation	others
ad.♂ - ad.♀	M 23 Th 2 D 33	Th 1 D 2 At 1	At 1	Th 1 D 2
ad.♂ - ad.♂	M 20 Th 1 D 2		At 1	
ad.♂ - young♀	M 1 Th 2 D 24 At 13 B 1		D 2 At 3	Th 1
ad.♂ - young♂	M 3 D 21 At 7 B 2	Th 2 D 1 At 1	Th 1 D 1 At 1	D 1
ad.♂ - baby	M 5 Th 1 At 5 B 1			
total	M 52 Th 6 D 80 At 25 B 4	Th 3 D 3 At 2	Th 1 D 3 At 6	Th 2 D 3

The duration of observations was 453 minutes.

Table 10. Comparison of the frequencies of aggressive interactions in the feeding area and those out of the feeding area.

traced individuals	adult females				adult males			
individuals involved in aggression	out of the feeding area *		in the feeding area **		out of the feeding area *		in the feeding area **	
	moving away	aggress-ion	moing away	aggress-ion	moving away	aggress-ion	moving away	aggress-ion
adult females ***	0.34	0.08	0.61	2.7	0.38	0.12	1.2	2.3
adult males	0.1	0.2	4.8	1.3	0.3	0.2	8.8	1.8
young females	0.07	0.08	0.3	0.2	0.09	0.18	0.04	1.8
young males	0.03	0.03	0.62	0.17	0.13	0.05	0.13	1.6
total ****	12.0	6.3	195	76	17.5	11.0	68	183

* Data from Table 5. ** Several afult females and males were continuously observed in the feeding area when they were foraging wheat grains given. *** (case No./10 hrs.) ÷ (number of members of each class) i.e. frequencies of aggressive interactions between any pairs of individuals of the classes. **** Total frequencies of aggressive interactions per 10 hours.

Table 11. Frequency distribution of individuals appearing in the circles centered by the traced individuals.

(The troop was staying in the neighborhood of the feeding area.)

diameters of circles	traced individuals	monkeys appearing in circles	numbers of monkeys in circles 0	1	2	3	4	5	6	7	8	9	12	13	14	16	18	20	total No. of monkeys	$S^2/\bar{x}$
20 meters	Imo	offspring	13	8	5	3														
		total - O - B	6	5	4	1	2	1	3	3	2		1		1		1			
		ad. ♀	15	5	4	2	1	3												
	Sasa	offspring	9	6	5	5	1	5												
		total - O -B	5	2	2	4	1	3	3	2	2			1	1	1	2	1		
		ad.♀	9	6	5	4	2		2	1		1								
	Imo + Sasa	total - O - B	11	7	6	5	3	4	6	5	4		1	1	2	1	3	1	312	5.38
		ad. ♀	24	11	9	6	3	3	2	1		1							102	2.51
10 meters	Imo	ad.♀	21	6	3															
	Sasa	ad. ♀	20	9	1															
	Imo + Sasa	ad.♀	41	15	4														23	0.97

Numbers in each cell indicate the frequencies of circles in which each group of monkeys was found.

Table 12. Correlation between the distances from a monkey and the numbers of monkeys found at these distances.

	traced individuals	Imo		Sasa	
	monkeys found around the traced individuals	adult females	young individuals	adult females	young individuals
the distances from the traced individuals to the monkeys found	0 - 0.5	0	1	0	0
	0.5 - 1	0	1	0	0
	1 - 1.5	0	4	0	0
	1.5 - 2	0	0	0	0
	2 - 2.5	2	2	0	0
	2.5 - 3	3	4	1	2
	3 - 4	3	6	4	5
	4 - 5	5	4	10	15
	5 - 6	8	10	11	23
	6 - 8	9	12	17	27
	8 - 10	12	27	20	32

Table 13. Frequency distribution of the numbers of individuals that appeared in the circles centered by the traced individuals. (The troop was moving and foraging.)

diameters of circles	traced individuals	numbers of individuals*						
		0	1	2	3	4	5	6
20 meters	Nashi	11**	4	2	1	0	2	0
	Imo	6	8	4	0	0	2	0
	Sasa	2	6	9	2	1	0	0
	total	19	18	15	3	1	4	0
10 meters	Nashi	17	3	0	0	0	0	0
	Imo	16	3	1	0	0	0	0
	Sasa	13	4	3	0	0	0	0
	total	46	10	4	0	0	0	0

* Numbers of the individuals that appeared in the circles except for babies and the offspring of traced individuals. ** Numbers in each cell indicate the frequencies of circles in which each group of monkeys was found. The total numbers of the circles investigated were 60 for each of the circles with 20- and 10-meter diameters.

Table 14. Density and the range of troop expansion at a certain moment, and the distance of movement per one hour.

state of the troop		ad ♂	ad ♀	young	offspring	baby	total -off.-b.	total -b.
staying in the neighbourhood of feeding area	density (/100 m²)	0.11	0.54	1.00	0.46	0.36	1.65	2.11
	the distance of movement (/1hr.) (m)	120	128	80			100	
	the range of troop expansion (x 100 m²)						53	
moving and foraging in their natural habitat	density (/100 m²)	0.03	0.11	0.29	0.14	0.19	0.43	
	the range of troop expansion (x 100 m²)						205	
age/sex composition of the troop		4	25	65	5		88	

Table 15. Density of staple food (numbers of woody plants / 100 m^2)

staple food scientific name	Japanese name	station 1	station 2	station 3	average
Machilus Thunbergii	tabunoki	14	2	7	4
Daphniphyllum Tejismanni	himeyuzuriha	8	2	0	1
Ficus erecta	inubiwa	2	1	3	2

Station 1 is on the slope facing the sea. Stations 2 and 3 are in the forest.

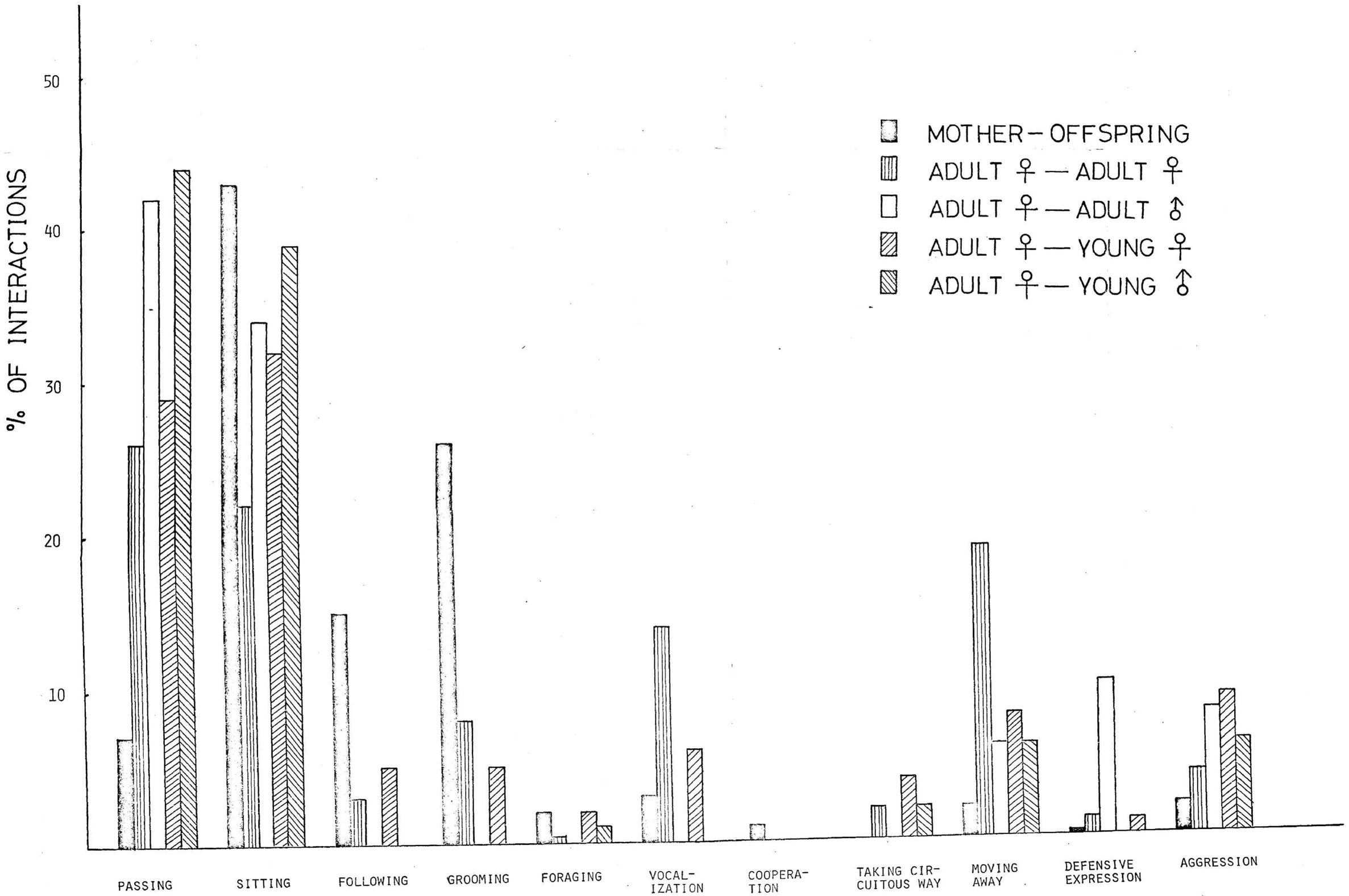

% OF INTERACTIONS
50
40
30
20
10
MOTHER – OFFSPRING
ADULT ♀ — ADULT ♀
ADULT ♀ — ADULT ♂
ADULT ♀ — YOUNG ♀
ADULT ♀ — YOUNG ♂
PASSING
SITTING
FOLLOWING
GROOMING
FORAGING
VOCAL-IZATION
COOPERA-TION
TAKING CIR-CUITOUS WAY
MOVING AWAY
DEFENSIVE EXPRESSION
AGGRESSION

Fig 1-a

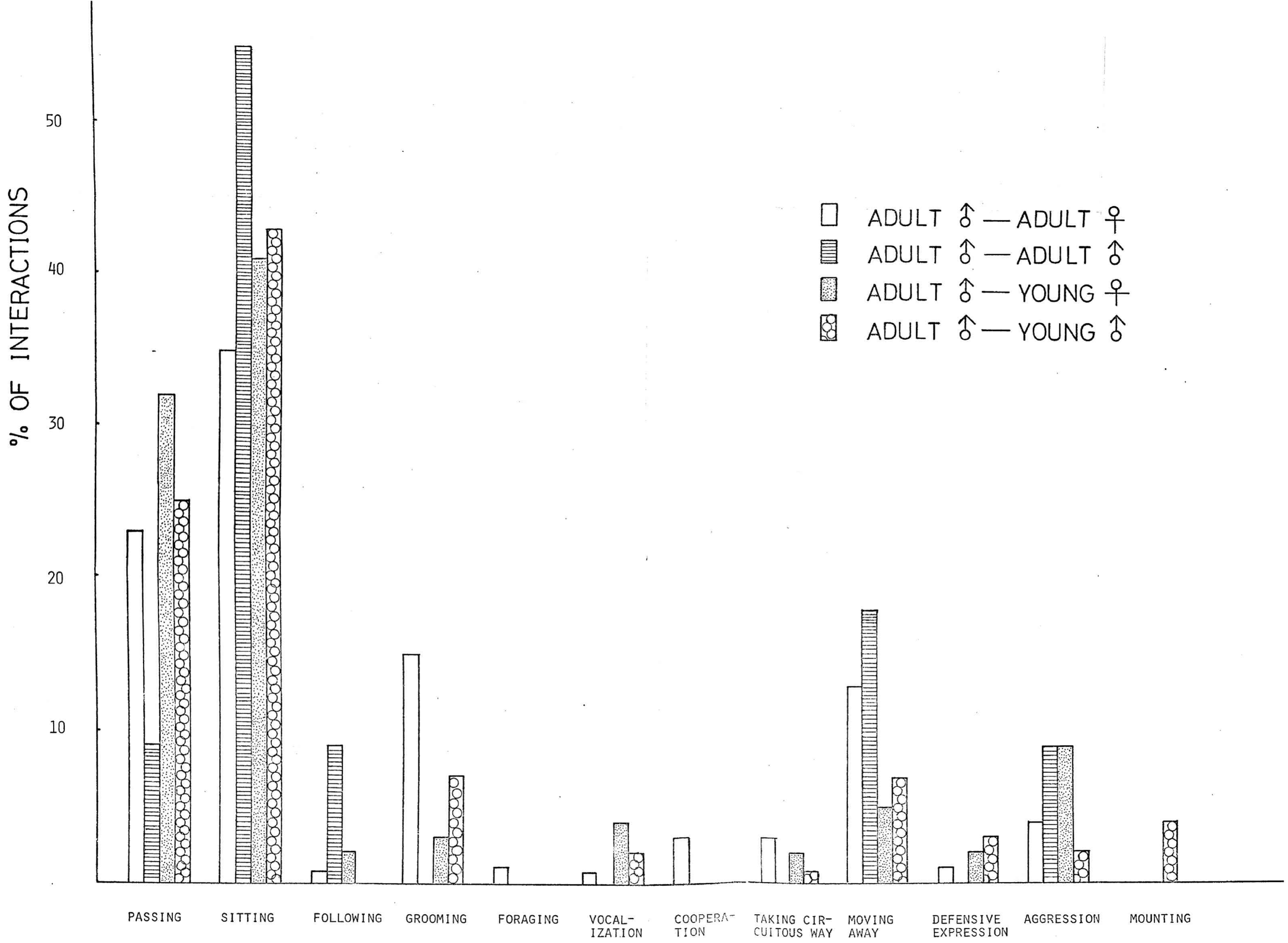
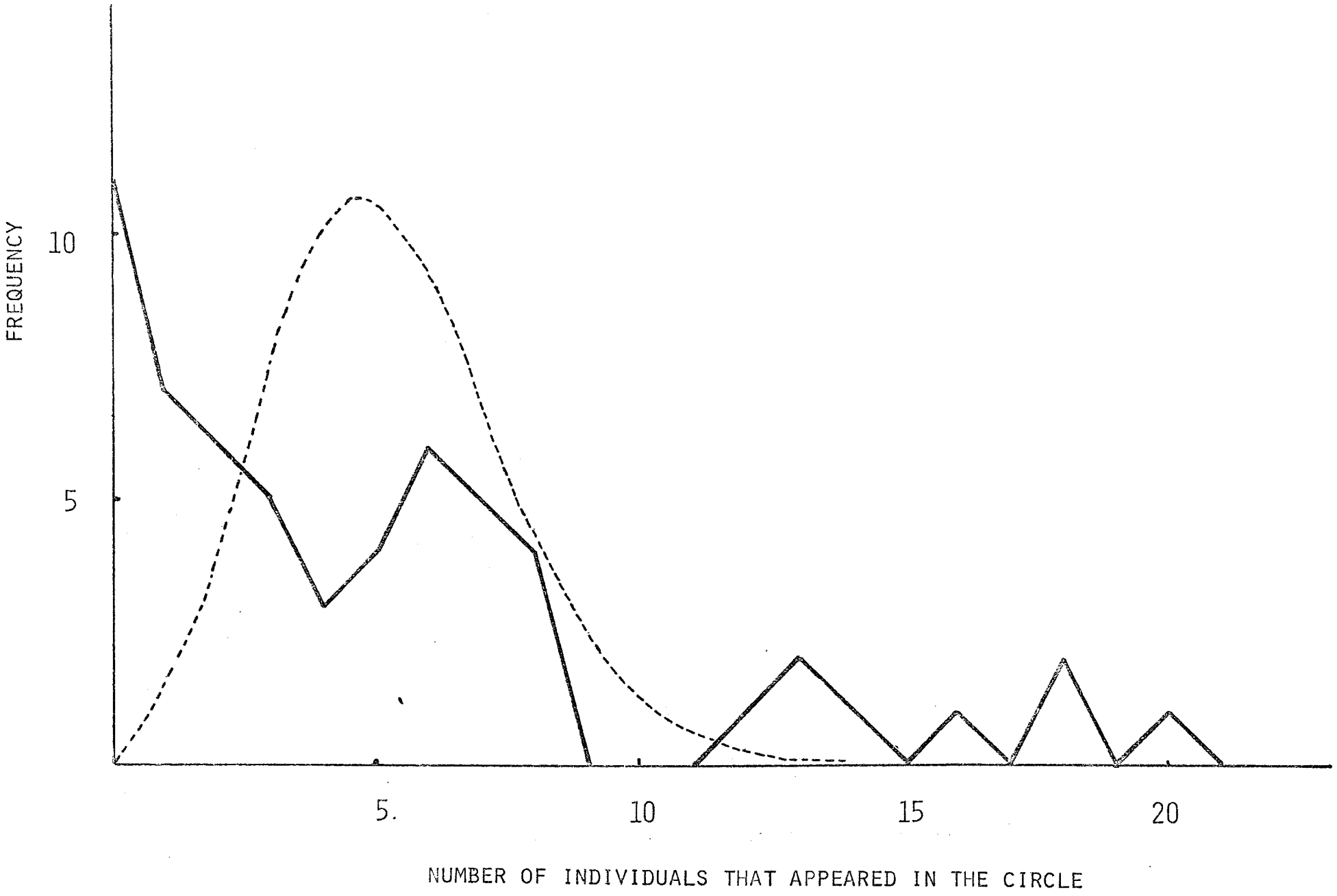
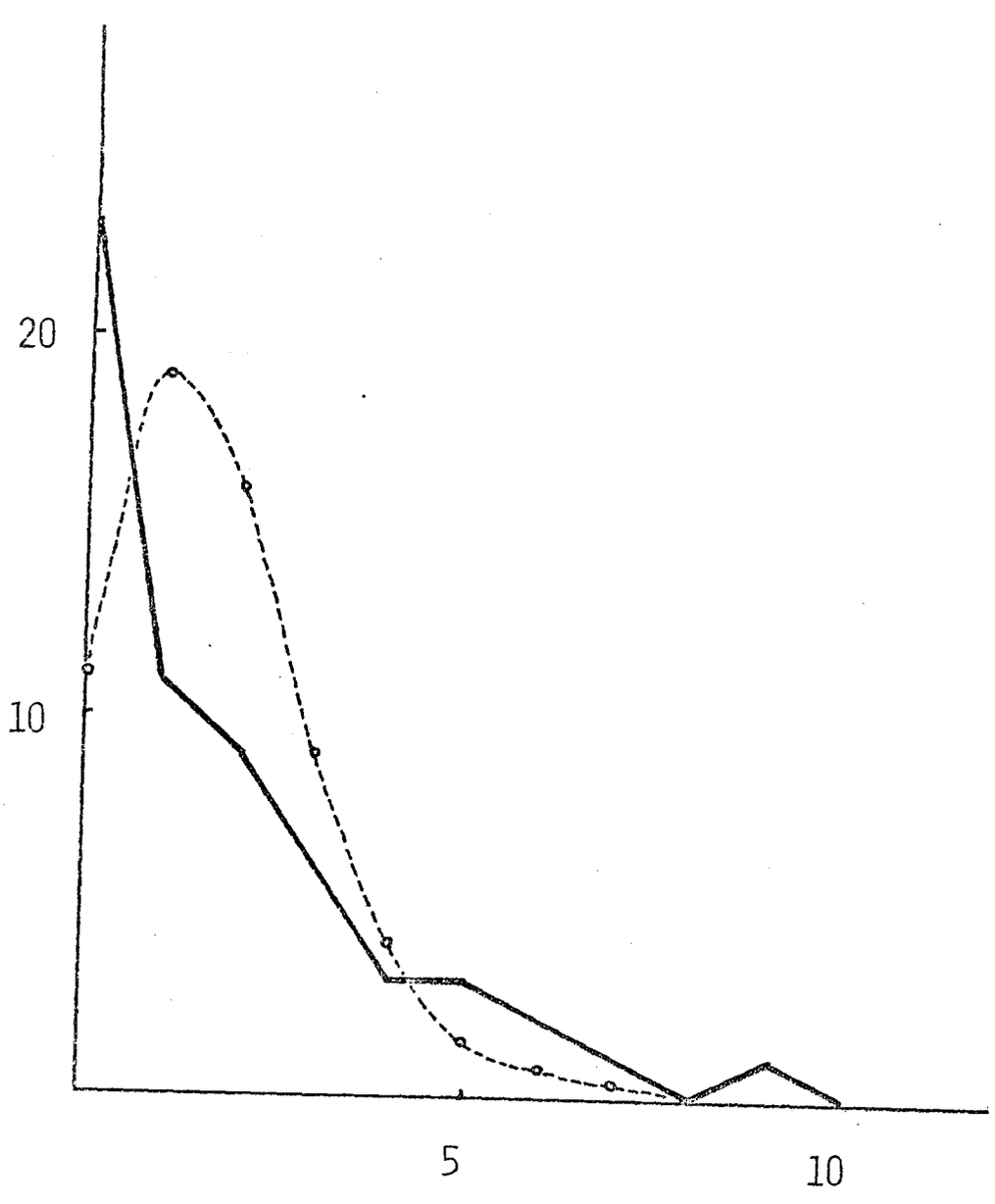

% OF INTERACTIONS
50
40
30
20
10
ADULT ♂ — ADULT ♀
ADULT ♂ — ADULT ♂
ADULT ♂ — YOUNG ♀
ADULT ♂ — YOUNG ♂
PASSING
SITTING
FOLLOWING
GROOMING
FORAGING
VOCAL-IZATION
COOPERA-TION
TAKING CIR-CUITOUS WAY
MOVING AWAY
DEFENSIVE EXPRESSION
AGGRESSION
MOUNTING

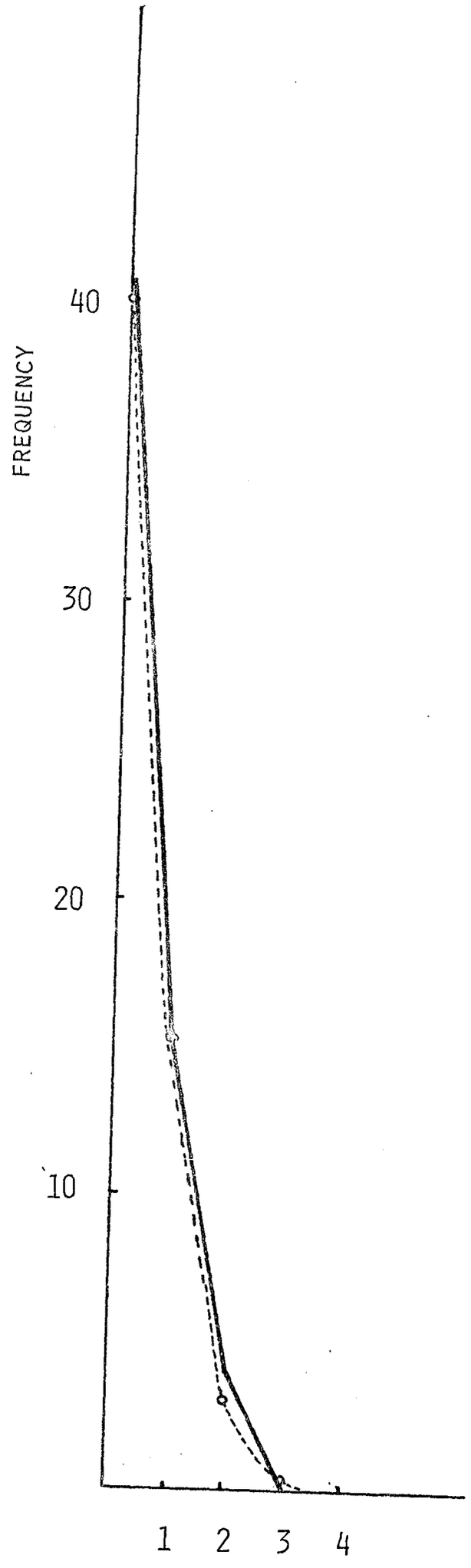
Fig 1-b


FREQUENCY
10
5
5.
10
15
20
NUMBER OF INDIVIDUALS THAT APPEARED IN THE CIRCLE



NUMBER OF ADULT FEMALES THAT APPEARED IN THE CIRCLE

(a)



NUMBER OF ADULT FEMALES THAT APPEARED IN THE CIRCLE

(b)

Fig. 3

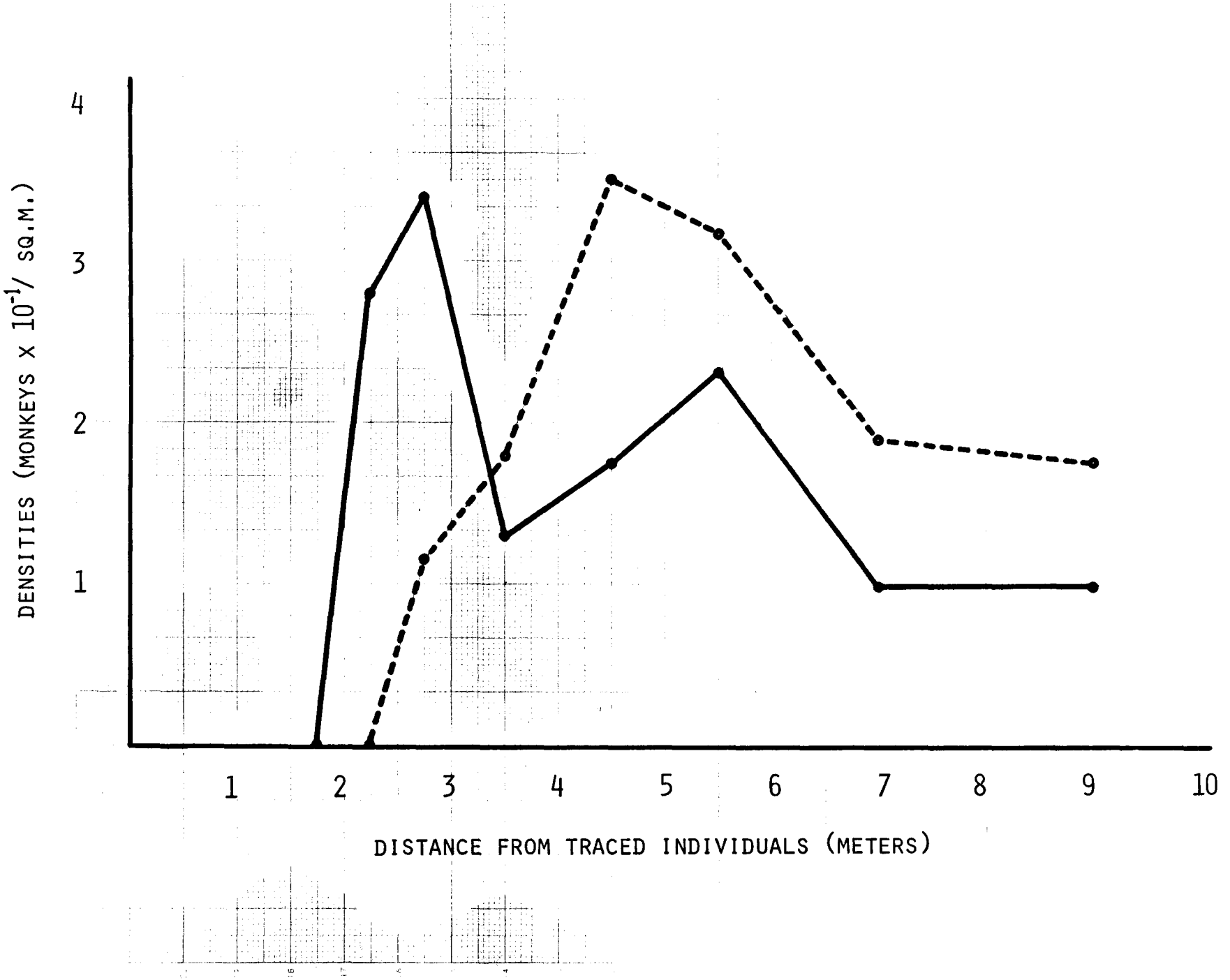

DENSITIES (MONKEYS x 10^{-1}/ SQ.M.)
4
3
2
1
1
2
3
4
5
6
7
8
9
10
DISTANCE FROM TRACED INDIVIDUALS (METERS)

Fig. 4

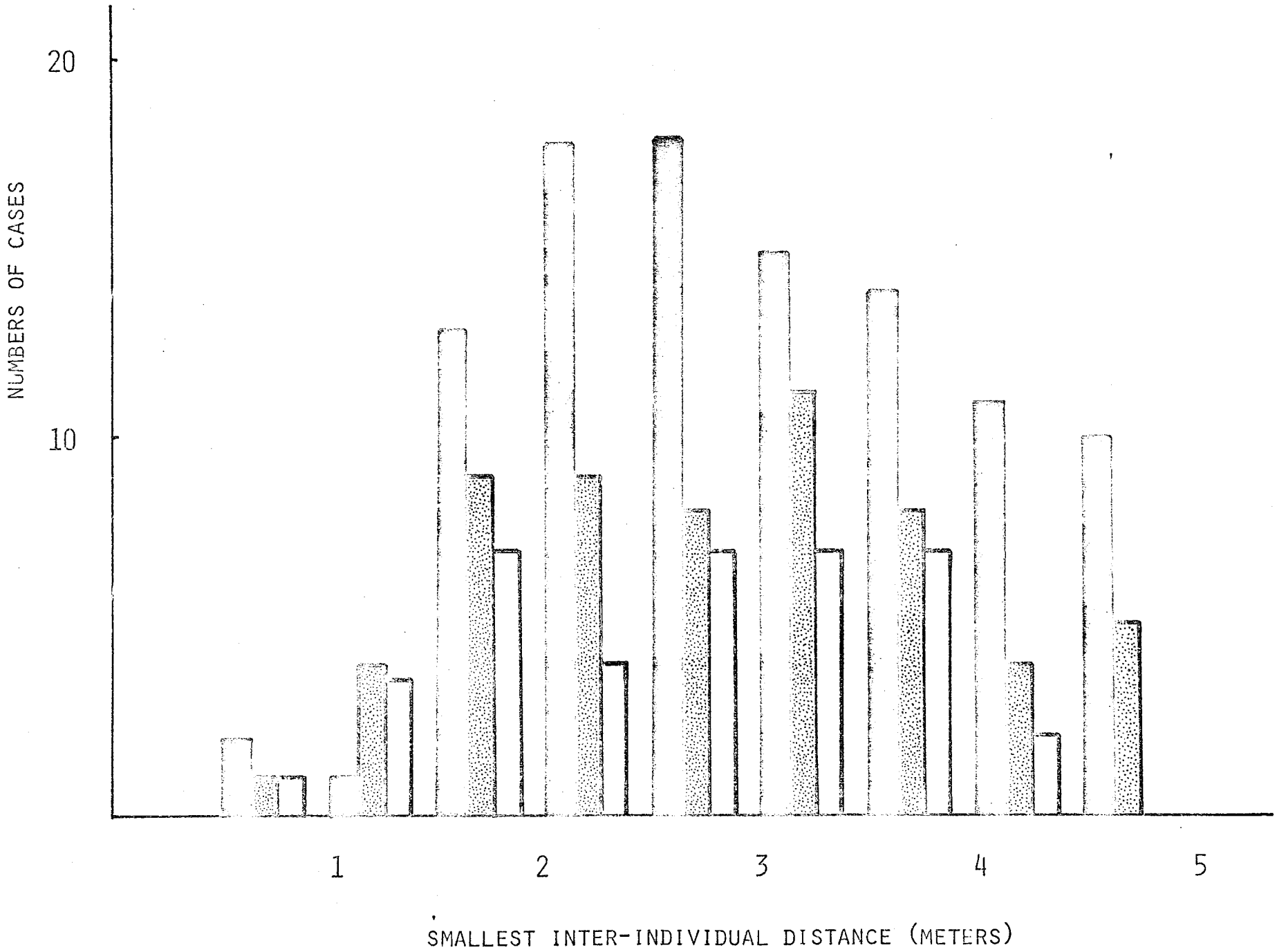
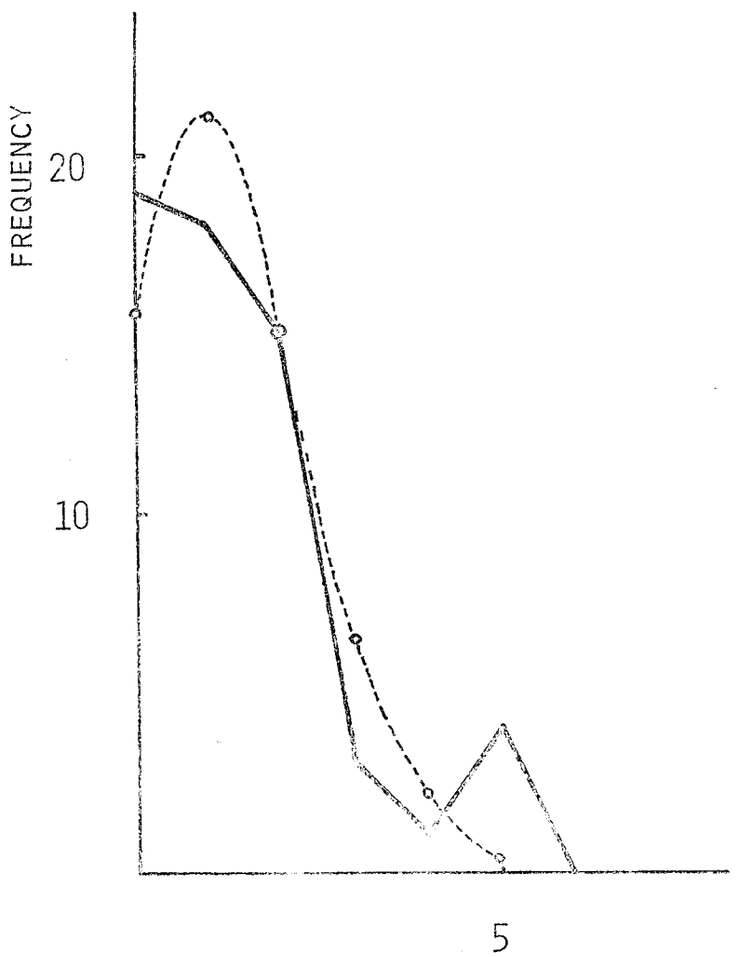
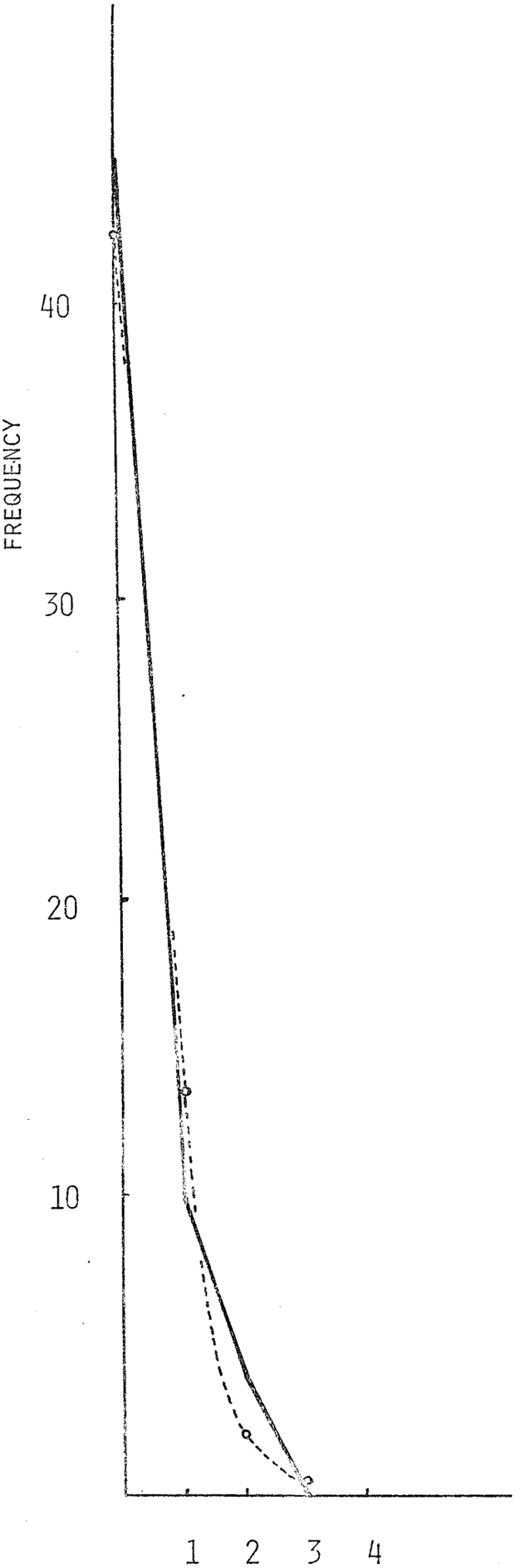

20
10
NUMBERS OF CASES
1
2
3
4
5
SMALLEST INTER-INDIVIDUAL DISTANCE (METERS)

Fig. 5

Fig. 6


FREQUENCY
20
10
5
NUMBER OF ADULT FEMALES THAT
APPEARED IN THE CIRCLE

(a)


FREQUENCY
40
30
20
10
1 2 3 4
NUMBER OF ADULT FEMALES THAT
APPEARED IN THE CIRCLE

(b)