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學位申請論文

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学位申請論文要旨

動物の集団を記述する現行の方法は、個体の空間分布様式を基準にして集団を認識・分類している。この方法は集団の命名・再認が容易であり、分布・生態などの研究において集団を記述する目的には便利である。しかし集団形成の帰結を基準としており、観察者の知覚特性に依存しているため、進化過程の分析には適さない。帰結の相違は過程の相違を反映するとは限らないし、進化過程における要素の重要性は観察者の知覚特性にとっての重要性・明確さと一致しないことがあるからである。たとえば、有効個体群は進化過程においてもっとも重要な役割を果たす「集団」のひとつであるが、現行の集団分類では記述できない。これらの欠点を補うためには、集団を認識する際にその形成要因に注目する必要がある。すなわち、採食効率・資源確保効率・交尾効率・育児効率の増加、被食率・病気罹患率の低減などである。集団の特性（構造や時空間サイズ）は各要因ごとに異なると考えられるので、進化過程を分析するためには、集団形成要因に従って集団を認識する必要がある。申請論文第1部では、このような用語法の利点と欠点を吟味し、導き出される予測と展望を考察した。

第2部では上記の諸点を確認するため、西アフリカ、ギニア共和国、ボツソウ保護区の野生チンパンジー (*Pan troglodytes verus*) のパーティー・サイズと、パーティー形成に影響すると予想される諸要因との関係を調べた。その結果、採食率とパーティー・サイズは負の相関を示し、危険な状況には大きなパーティーを形成する傾向があった。また、発情メスはオスの集中を引き起こした。子供を持つ授乳中のメスが単独で過ごす傾向は皆無ではないものの、ゴンベの先行研究で報告されたほど顕著ではなかった。これらのことから、チンパンジーのパーティー形成（離合集散）には採食だけでなくさまざまな要因が関与しており、集団構成を統一的に記述するには要因による分類の方が合理的であると考えられる。

(以上)

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ON THE CONCEPT OF "GROUP" OF ANIMALS, WITH SPECIAL REFERENCE TO
NON-HUMAN PRIMATES: A PROPOSAL OF THE PLURALISTIC TERMINOLOGY

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SUMMARY

In the current terminology for animal groups, spatial distribution of organism individuals is used as a criterion for the description and classification of groups. The merit of this method is its ease of giving a name to a group and its latter recognition, so that it suits to describe the groups in the context of studies of distribution and/or ecology. However, the method is not good for analyzing the evolutionary process, because it treats the consequence, not the process, of group formation, and it depends on the peculiarity of human perception: the difference among consequence patterns does not always reflect the difference among process patterns and the important factors during the evolutionary process is not always clear for human perception. The current method has some difficulties for describing the effective population, of which role is one of the most important for the evolutionary process. In order to eliminate such demerits, it seems to be necessary to focus on the factors affecting the group formations, i.e., decreasing predation pressure and contraction of disease, and increasing the efficiency of foraging, resource defense, copulation, and rearing. Each factor produces a group of a different nature (structure, duration and size), so that we need to recognize and classify groups according to these factors. The merits and demerits of such new terminology is discussed, and the estimation and perspectives for future studies are examined.

Key words: animal groups, terminology, evolution, pluralism, human perception, non-human primates

INTRODUCTION

"Living in groups" is one of the most important concepts in the context of studying animal behavior, evolution, ecology, and life history. There are so many animal species living in groups that the analysis of group forming factors is a central issue in modern behavioral ecology (e.g., E.O. Wilson, 1975; Rubenstein & Wrangham, 1986; Krebs & Davies, 1987). However, the concept of group for "living in groups" has not been clearly defined. In general, "group" is regarded as "any set of organisms, belonging to the same species, that remain together for a period of time while interacting with one another to a distinctly greater degree than with other conspecific organisms" (E.O. Wilson, 1975, p.585), and many everyday terms have been used to describe group, e.g., school, herd, troop, pride, party. The usage of everyday terms represents the great role of the property of human perception in description and classification of groups. Such a method makes it easy to describe and to recognize groups in the studies of distribution and ecology. We can justify it within such context, as far as its usage is restricted.

On the other hand, some difficulties in the method are caused by the "propensity" of human perception. For example, breeding systems containing one male and plural females are often referred to as "harems," but their structure and size vary too much to be described by one word (Wrangham & Rubenstein, 1986). The current terminology (CT) would face greater difficulty in the study of evolution of groups. There is no guarantee that the traits which clearly appealed to human perception performed a great role in the evolutionary process (Hull, 1981; Dawkins, 1982; Kawata, 1987, in press; Kitcher, 1989). Genes, the most fundamental factors in the evolutionary process, have been concealed by the organism, the most evident factor for human perception. It could be the case for the recognition of groups. The groups evidence for human perception, such as herd, pride, have not always performed an important role during

the evolutionary process. We cannot suppose that they have (Kawata, in press). The preceding studies for the effective population size (N_e) are a typical example. N_e represents the number of individuals belonging to a Mendelian population in which any individual contributes equally to gene frequency in the next generation. Effective population is the "group" of important roles in the evolutionary process: in the smaller N_e , the contribution of genetic drift becomes larger, and also the inbreeding ratio increases. Therefore, N_e directly affects the evolutionary process. We cannot, however, measure N_e through direct observation, because N_e is usually a smaller size than the directly observed group size. N_e has been estimated in rather few species, e.g., house mice, deer mice, sparrows, lizards (see E.O. Wilson, 1975; Chepko-Sade & Shields, 1987 for reviews. The latter estimates N_e of some species of mammals, such as bears and wolves, using data collected under good conditions and some methods of estimation. For N_e of non-human primates, see section III-3).

These points reveal that the current terminology (CT) is, at least in part, inadequate for the studies of evolutionary process. The aim of this paper is to examine the other view point for description of groups, which is more adequate for evolutionary studies. I will restrict the materials for discussion within non-human primates, although I believe that the view point presented here is, logically, applicable to all of the animal species. The reason that non-human primates are suitable animals for discussing the concept of group is because of their highly organized social systems and diversity of group structure (Smuts et al., 1987).

In the first section, I will review the characters of CT for describing non-human primate groups. In the next, demerits of it will be discussed. Some kinds of factors, such as decreasing predation pressure and increasing reproductive efficiency, can be supposed as affecting group formation. Natural selection acts differently for each factor, so that each factor produces its proper group. In fact, the structure of the

breeding system and the foraging system in a given species usually differ from one another, and the social system does not represent the effective population. Therefore, in the context of evolutionary studies, the social system cannot be regarded as *the* group system of a species. In the third and last section, presented will be the pluralistic concept of group, which eliminates such difficulties of CT. In the context of evolutionary studies, the factors forming groups should be treated. I will also discuss the merits and demerits of the method and some estimations and perspectives, as well as its relation with effective population and social systems.

I. SOME CHARACTERS OF CURRENT TERMINOLOGY

The description of "something (e.g., group of animals) exists" is always loaded by a background-theory or inclination of observer's perception (Hanson, 1969). We can regard anything as an "entity," in one sense, so that a criterion is necessary when we choose finite "real" entities from theoretically infinite options. This application is not always done consciously. In the case of the description of the groups, it seems to be performed often unconsciously. The constraint and peculiarity of human temporal-spatial perception acts as the criterion in such case. For analyzing description systems, it is necessary to clarify the background theory of a description. Therefore, I will discuss the background theory of CT of groups.

Some of the main terms used for describing the groups of non-human primates are summarized in Table 1. The terms are classified and named according to disuniformity of spacio-distribution of individual animals. Many individuals gathering in a narrow area are referred to as a "group," and a few dispersed in a wide area as "solitaries." In other words, CT is not used according to the causes of group formation, but the consequences of it.

The process of recognition of groups, by which CT seems to be supported, is regarded as follows. Although Hinde (1976) also analyzes the similar process, his scheme is intended for behavioral or sociological studies, while the scheme described here is for evolutionary studies. In general, a criterion for introducing the concept of "group" is disuniformity in distribution density of individual animals (cf. Popper, 1959; Watanabe, 1969, 1985). What is the disuniformity in distribution density? Now, suppose that inter-individual distances (IIDs) are used as the measure for distribution density (Waburton & Lazarus, 1991). When the distribution of IIDs represents more than one type of function, among which mean and variance differ, spacio-distribution density can be regarded as disuniform (Figure 1). The set of individuals is called a "group", of which IIDs belonging to a function of smaller mean and variance. When x represents IIDs, and f and g the two functions,

$$(x_f < x_g) \cup (\sigma_f < \sigma_g) \text{ ---> } x \text{ disuniform} \text{ ----- (1)}$$

and the set of individuals belonging to the variable range of x would be recognized as a group.

Figure 2 schemes this function on a two-dimensional space. The distribution of individuals is uniform (Figure 2a), or random (Figure 2b). In such cases, observers describe no group. While, the case of disuniform distribution of individuals (Figure 2c), they recognize the existence of groups, the sets of individuals of which spacio-distribution densities are higher and more uniform (dotted circles).

In some cases, not spacio-distribution but affinity among individuals are used; especially for the recognition of "society." However, affinity and disuniformity among spacio-distribution are fundamentally equivalent. When we do not treat individual varieties, both are completely the same. Spacio-distribution is generally a good measure of affinity, or they correlate to a high degree, because the frequencies of allo-grooming or of spatial proximity are usually used as measures of

affinity (e.g., Takahata, 1982; Smuts, 1985). Spatial proximity is nothing else than the intimate spatio-distribution, and allo-grooming always attached with spatial proximity so that its frequency would reflect on spatio-distribution. In fact, "group" fission in macaque species reflected individual affinity measured in grooming interactions (Chepko-Sade, 1979; Oi, 1988). In some aspects, social affinity is a less suitable criterion than spatio-distribution: measuring the former is more difficult than measuring the latter. Considering these points, the following discussion will be limited to spatio-distribution.

This recognition process, using disuniformity of spatio-distribution of individuals, treating the consequences of group formation, has some merits as well as demerits. The latter will be discussed in the next section.

The first of its merits is its facility for usage. Naming of groups are so easy according to this method: if some animals forage together, we can find the existence of a group and give a name to it according to the number of animals and the degree of their dispersal. Secondly, recognition of the group is also easy. This comes from the uniformity of the perception ability among humans. Some of the terms listed in Table 1 were introduced by the first students of the species, and have been used until now: for example, the terminology for hamadryas baboons was established by Kummer (1968), the first researcher of them, and it is still in use. If inter-observer variation of the recognition process was high, such a method could not stand.

However, the temporal-spatial-criteria of disuniformity is not clear. Many "non-troop" males approach and enter a troop of Japanese macaques during their copulatory seasons. The frequency of the appearance of such males were continuous, from high to low (Figure 3). This makes it impossible to divide "non-troop" and "in-troop" males. Furthermore, some of the "non-troop" males would remain until next non-copulatory season,

and would become "in-troop" males (Sugiyama, 1976). Until when were they "non-troop" and from when "in-troop?" ---- who knows? The CT seems to adopt "human recognition ability" as a criterion. This is apparently *petitio principii*, but considering problem of explanation ability and problem presentation ability, it seems to be impossible to define "groups" without *petitio principii*. On the other hand, such fuzzy criteria may represent the fuzziness of the group itself. If this is right, the ambiguity is not a demerit, but a postulate for describing groups.

In summary, CT is effective in some cases, such as the census of population density, because it is one in which our properties of perception will not bias the process so much. And also, even in the studies on animal ecology or behavior, as long as grouping formation itself is not the object of analysis, or as long as the existence of groups is treated as an dependent variable, CT has great efficiency. However, it is not be applicable to the phenomena beyond our perceive ability: evolution, for example. Evolutionary changes, in general, go under much longer time spans, than are suitable for human perception. This is the theme of the next section.

II. DEMERITS OF THE CURRENT TERMINOLOGY

The important points in evolutionary studies are how some traits affect the change of gene frequency in the next generation. The characteristics of the "path" are not simple, through which the spatio-distribution of the individuals effect on the structure of the next generation's gene pool: the relation among the two would be complicated (Kawata, in press). Forming organized group affect the effective population size in many ways (Chepko-Sade & Shields, 1987). *Not* even organized distribution (uniform one) can affect the next generation's gene frequency, e.g., through local mate competition. Therefore, CT according to disuniformity of individual distribution may conceal the existence of

"groups" which performed a greater role during the evolutionary process. D.S. Wilson (1983), emphasizing the contribution of group selection, states that reciprocal altruism and hawk-dove game should be explained by the intra-demic selection mechanisms. It is apparent that the concept of "group" in the evolutionary context differs from that of the socio-ecological context, although I do not agree with D.S. Wilson's argument because I think his points are semantic ones.

In this paper, I suppose all groups have been evolutionarily formed through natural selection. This assumption has not been strictly proven, but many authors have shown its appropriateness (E.O. Wilson, 1975; Brown, 1983; Wrangham, 1983, 1987; Wrangham & Rubenstein, 1986; Dunbar, 1988). From this assumption and the fact that the individual is regarded as the "unit" of groups, factors forming groups should increase at least the survival or the reproductive probabilities of the members. This is equivalent that groups will be regarded as "vehicles" of replicators on which selection acts (Dawkins, 1982). The followings are the group forming factors which increase individual survival probabilities: protecting against predation pressures and decreasing the rate of contraction of a disease, and gaining resource defense and foraging efficiency. Concerning reproductive probabilities: increasing copulation and rearing efficiencies (for the ground and character of each factor, see Wrangham, 1983, 1987; Dunbar, 1988). What kinds of groups would be produced by each factor (Table 2)?

First, the larger group has the larger effect of anti-predation. The large number of individuals make precautions and patrolling easier (van Schaik et al., 1983; de Ruiter, 1986) and the large size of the groups itself may have some effect on anti-predation (van Schaik & Nordwijk, 1985; Anderson, 1982; Kummer, et al., 1985). These effect, however, diminish as the group size increases. Then, fitness function against group size will show a convex logarithm curve.

Secondly, the case is rather different for the resource defence efficiency. Group size affects territory defence and inter group dominance relations (Oates, 1977; Struhsaker, 1967; Hamilton et al., 1975, 1976; Dittus, 1986). However, the efficiency decreases in very large groups, because *intra*-group competition become greater than *inter*-group competition (Janson, 1985). Therefore, fitness function makes the Gaussian curve with its extreme value correspond to the middle or large size of group (van Schaik, 1983; Dunbar, 1988).

Forming groups can increase foraging efficiency because it avoids exhausting one feeding patch (Terbough, 1983), makes possible the exchange of information regarding feeding patches (Kummer, 1968; Wrangham, 1977; Dittus, 1984), and increases predation efficiency (Boesch & Boesch, 1989). However, a very large group size introduces *intra*-group feeding competition which decreases individual fitness (Wrangham, 1981; de Ruiter, 1986). Therefore, the optimal size for foraging groups is rather small. It is controversial whether fitness function against group size is monotone decrease or Gaussian curve (Krebs & Davies, 1987). If the efficiency of finding feeding patches increase through information exchange with other group members, the function will be the Gaussian curve. If there is severe competition among group members, and the positive effect of forming the group is small, it will be monotone decrease.

The hypothesis that animals form groups to guard against disease seems to be suitable for non-human primates, because *allo*-grooming behavior among them has hygienic functions as well as social ones (Goosen, 1981). They groom often the parts of the other members where groomees cannot self-groom (Hutchins & Barash, 1976). It is possible that large numbers of group members increase the frequency of being groomed, and as a result, the rate of contraction decreases. There is, however, the maximum number of individuals as groomers for one

individual and time budget is also limited (Dunbar, 1984). Thus, the effect of group size saturates at some level. Furthermore, the members in large sized groups can more easily contract infectious disease. Therefore, the fitness function of anti disease effect against group sizes will be the Gaussian curve.

Copulation efficiency directly affects reproductive success. When the number of females in a group increases, copulatory success of males also will increase. And when the number of males increase, females can more easily choose their consort partner. Too many individuals, however, introduce mate competition and decrease copulatory efficiency. In fact, copulatory success correlates negatively with group sizes (van Schaik, 1983). And group forming during non-copulatory seasons is not always explained as pre- or post-copulation guarding (Ridley, 1986). These degrees and patterns of competition can affect the optimal group size, nevertheless, the shape of the fitness function would not be affected because a copulation needs at least two animals, a male and a female.

The effect of increase of rearing efficiency seems to be more remarkable in non-human primates, because allo-mothering behavior for infants by individuals other than the mothers have been widely observed (e.g., Hasegawa & Hiraiwa, 1980; Silk, 1982; Smuts, 1985). Forming groups increases the frequency of being nursed by such animals, and the probability of infant survival increases as a consequence. However, if there are a few helpers in a group, such effect saturates. Thus, this factor cannot produce groups of large size. Tamarins have only two or three helpers in a group (Goldizen, 1987), and lactating chimpanzee females tend to spend more time alone than others (Wrangham & Smuts, 1980). Therefore, it is adequate to suppose this effect saturates according to the smaller size of group. If infanticide occurs in a group, infant survivorship is threatened in large sized groups. The fitness function is represented by a Gaussian curve in such a case.

In summary, different factors produce different groups: different in their structure (size and composition). Therefore, the method describing non-human groups monistically, like "multi-male and multi-female" or "monogamous pair," is limited in its usage: it can be used in the context in which group forming factors can be neglected. It is equivalent that such methods can not be used in the study of evolution, if its criterion is not mentioned.

It has been revealed that CT is not suitable for the study of evolution because of the following two points. First, inter-species comparison is difficult within CT. Second, CT cannot describe adequately the grouping of species which have variable group sizes, which includes almost all non-human primate species.

The first problem does not occur in the single species. Groups belonging to a single species have been sharing common evolutionary history for a long time, and the groups described with same term should have the almost same function, as far as the observers's recognition ability does not strikingly differ, although it is not clear whether such groups have performed important role during an evolutionary process. However, the individuals belonging to different species have been through different evolutionary paths. Therefore, the groups appearing to have nearly the same structure for observers does not always have same functions in the aspects of evolution, ecology and sociology. On the other hand, the difference of size and composition among groups does not guarantee the difference of function. Redcolobus monkeys forage in a group of some dozen animals (Struhsaker, 1975), while orangutans tend to do so alone (McKinnon, 1974; Rodman, 1977). These large group and solitary animal are equivalent concerning the point of the function of "feeding." Another example comes from the structure of breeding groups. While siamangs copulate and breed in a group of monogamous pair (Chivers, 1974), macaque monkeys do so in a large group of multi-male

and multi-female (Caldecott, 1986). Both of them have the same function.

The second problem is that CT has difficulties in describing variable group structure. This point can be ideally eliminated by considering the usage of terminology, but, actually, terms are often used out of such considerations and biased the following usages. Orangutans, for example, are sometimes described as "solitaries" because of their foraging pattern, but they form polygamous "group" for breeding (Galdikas, 1981; Mitani, 1985). Emphasizing the breeding system, it is possible to regard them as "polygamists," but this is seldom the case. Blue monkeys live in polygamous groups during non-copulatory seasons, but in multi-male and multi-female groups during copulatory seasons, as a consequence of entering of "non-troop" males (Tsingalia & Rowell, 1984). The pattern is the same for Red-tailed monkeys (Cords, 1984) and patas monkeys (Chism & Rowell, 1986; H. Ohsawa, personal communication). Some baboons change their group size between the foraging phase and the sleeping phase (Stammach, 1987). The composition of groups of mountain gorillas shift chronologically from monogamous pairs to multi-male groups, through polygamous groups (Fossey, 1983; Yamagiwa, 1987). The CT (current terminology) has difficulty in describing these cases. There is no reason, at least, that one of the group structures should be emphasized between the foraging phase and the breeding phase. Nevertheless, "forest guenons and patas monkeys have been seen as exemplars of a one-male-group type of social structure" (Cords, 1987: p.107). To improve such a point of view, Cords (1987) introduces the term, "polygynous one-male." However, this complex-expression, I think, symbolizes that CT is going bankrupt. The comparison between "one-male" and "multi-male" groups under such classification is a semantic one (see also Itani, 1972, 1985).

III. PRESENTATION OF NEW CONCEPT AND TERMINOLOGY

III-1. A viewpoint of describing groups in a pluralistic way

As we have seen, CT has some difficulties in the context of evolutionary studies. Thus, another viewpoint which clears up such difficulties is necessary for the aim of the study of evolution. Emphasizing factors of group formation is the simplest way. If a focal group has been formed to protect against predation pressure, it can be called "anti-predation group," and for a group of increasing feeding efficiency, "feeding group" is a possible label. In geladas, their one-male unit (OMU) seems to correspond to breeding unit, and their herd seems to have some ecological function (Kawai et al., 1983; Dunbar, 1984, 1988, 1989). Thus, it is possible to call this group a "breeding group" instead of OMU and "anti-predation group" instead of herd.

This pluralistic terminology (PT) does not require the physical aspect of spatial distribution of individuals as its necessary condition. While the properties of human perception affect the recognition of spatial distribution of animals, classification by group forming factors can minimize such effects. Although, to sweep away this "bias" is impossible, I believe that less is better (cf. Churchland, 1979).

As mentioned in Section II, different factors produce different groups. Therefore, a pluralistic and parallel pattern is shown in a general scheme of the structure of groups classified by their function. The membership of each group is not necessarily constant, and the groups can exist in diachronic patterns as well as synchronic ones. A focal animal can belong to several different groups at one time, and it belongs to group A at the time t_1 but to group B at t_2 . The scheme shown in Figure 4 is a synchronic one at a given hour. A diachronic scheme of the structure can be drawn as an expansion of Figure 4 into three dimensions, although it is too complicated to discuss here.

I believe that PT for describing groups can exclude the

difficulties of CT. First, there is no need of sub-procedures when comparing among species. As mentioned above, CT needs some consideration concerning ecological and constraint conditions to compare groups among species, because groups having the same functions can appear to have different structures in different species. The comparison between "one-male group and multi-male group" is not so useful, and the pluralistic system makes it easy to compare "one-male *breeding groups* and multi-male *breeding groups*." Second, the pluralistic system can describe groups of species in which the structures of breeding groups, feeding groups and anti-predation groups differ from each other. It is not necessary to describe the groups of patas and blue monkeys using unnatural terms, such as "polygynous one-male." The system allows one to use a simpler description, "one-male multi-female feeding group and multi-male and multi-female breeding group." The latter form can be changed when other factors affecting group formation are revealed. CT has much difficulty in coping with, say, nine kind of groups in a species.

III-2. Merits of the pluralistic group view point

The view point of regarding groups pluralistically allows one to analyze a variety of group compositions among several species from a single common aspect.

Firstly, I will discuss the fission-fusion, temporal change of group size and composition, of forest primates (e.g., chimpanzees: Goodall, 1968; Nishida, 1968; Sugiyama, 1968; crab-eating macaques: van Schaik et al., 1983; mandrills: Kudo, 1987; spider monkeys: Symington, 1988, 1990). Fission-fusion can be regarded as "adjustment" of the sizes of groups for feeding, breeding, rearing, and so on (Sugiyama, 1990; Sakura, 1991, in prep). Furthermore, macaque monkeys, considered to form stable large groups of multi-male and multi-female, change group composition as seen above: the number of males increase during copulatory seasons (Figure

3). From the point of view of PT, both of the entering of the "non-troop" males of Japanese macaques and "fission-fusion" in chimpanzees or spider monkeys are located in the same continuum. Although Japanese macaques and rhesus macaques *seem* to form stable groups, they increase the size of breeding groups and decrease that of feeding groups: their groups also have fission-fusion character, even though it occurs on a far smaller scale than in chimpanzees and spider monkeys. In fact, Japanese macaques living in deteriorated habitat conditions divide their feeding groups into smaller size than usual, and they gather again on the feeding ground (Fukuda, 1983).

Stable multi-level group structure in hamadryas baboons and geladas is the second point (see Table 1). A multi-level society can also be regarded as an adjustment of group sizes between variable functions, like fission-fusion (cf. Kummer, 1968). They also form smaller groups for feeding and larger ones for anti-predation. The difference between fission-fusion in chimps and spider monkeys and the multi-level societies in hamadryas and geladas is the degree of stable membership: the former changes membership in a shorter time period, while the latter has a stable membership for a longer period (see below). According to PT, inter-specific variation of group structure can be regarded as the question of the degree of "discrepancy" between each functional group. And it allows one to locate the varieties of group structure into one continuum and to compare them; those of chimps, spider monkeys, macaques, geladas, hamadryas, and so forth.

Thirdly, it can also analyze inter-specific mixed groups in arboreal monkeys and New World monkeys. Inter-specific mixed groups (Gartlan & Struhsaker, 1972; Terbough, 1983; Mitani, 1991) are functional group(s) formed by the individuals coming from more than one species. Hence, according to the pluralistic terminology, it can be discussed in the same aspect of macaque grouping patterns. Plural groups are not necessarily

closed within a "species." Some authors attribute the causes of inter-specific mixed groups to anti-predation (Struhsaker & Gartlan, 1972) or feeding efficiency (Mitani, 1991). In other words, they form their anti-predation or feeding groups with animals of other species, or "inter-species fission-fusion." It is reasonable to form some functional group in such a way, if group forming within one species has some disadvantages. In arboreal monkeys, the optimal breeding group size may be smaller than the optimal feeding or anti-predation group size (Mitani, 1991). Then, they form inter-specific mixed groups for feeding or anti-predation, to eliminate the discrepancy (Sugiyama, 1990). In chimpanzees, on the other hand, their optimal group size may be larger for breeding than for feeding; they divide their feeding groups within a species. Chimpanzees, in fact, "adjust" their party sizes according to several factors: smaller parties for feeding and larger ones for breeding (Tutin et al., 1983; Sakura, in prep). This fact is circumstantial evidence for the hypothesis presented here, although strict confirmation needs more data for energy consumption and biomass of chimpanzees. The pluralistic terminology allows us to locate inter-specific mixed group and fission-fusion in one continuum.

The fourth perspective concerns the division of social groups and the inter-group transfer of individuals. These two, from the pluralistic perspective, could be regarded as long-term and wide-range adjustments of group sizes: large-scale fission-fusions. As Moore (1984) points out, group division and emigration of individuals are equivalent when group size is small. In one sense, this is the case when group size is large. The division of the social group changes the structures of the anti-predation group and the resource defence group, but its effects on the structure of the breeding group and genetic diversity are not constant because they depend on the patterns of division and the demographic history. While genetic diversities among social groups do not increase

through random divisions, it does in the cases in which the units of divisions are lineages (Melnick & Pearl, 1987). In these points, emigration of individuals has the same functions: random emigration does not increase genetic diversities among social groups, while non-random dispersion does (Melnick & Pearl, 1987). Therefore the functions of group divisions and individual emigrations is similar. However, emigrations do not affect on the feeding and rearing groups as much as divisions. If the mother group size is large enough, such effect by the emigration of one animal would be negligible.

Emigration is functionally equivalent to group division. Therefore, immigration is similar to group fusion. The fusion of social groups, however, has scarcely been reported, in contrast to many observations on divisions (Dunbar, 1987; Melnick & Pearl, 1987). Concerning individual transfer, both emigration and immigration have been observed frequently (Pusey & Packer, 1987). This difference among group fusion and individual immigration may be caused because the latter has less affect on the composition and size of feeding (rearing, etc.) groups. If such is indeed the case, the following two prediction can be made. First, in the species of rather large social groups, like macaques immigration into small groups would be less frequent than that into large ones. The reason is that the former could change feeding group structures more than the latter. Second, group fusion would be possible in a declining population when food availability is greater. All group divisions observed are in growing populations (Dunbar, 1987), and in such case, it is necessary to divide feeding groups into smaller sizes. In contrast, animals belonging to a declining population with enough food availability form larger anti-predation groups. Fukuda's (1983) observation on group fusion in Japanese macaques in Hakone, Honshu Island, Japan, may support this prediction.

III-3. Perspectives and problems in the pluralistic terminology

Here, I will discuss two problems with PT. First, the relation with effective population; Second, the problem of stable membership.

The first problem concerns breeding groups in PT. As mentioned above, effective population is one of the most important aspects of groups in the evolutionary process, but its size (N_e) has been measured only in a few species of non-human primates, e.g., Japanese macaques (Nozawa, 1991). Measurement of N_e in non-human primates is complicated because of overlapped generations. Firstly, it is necessary to measure the effective (genetic) migration rates. Sade et al. (1987) developed a method of measuring the rates among age-structured populations, and applied it to the rhesus macaques in Cayo Santiago Island. For the application of their method, some difficulties, e.g., distinction between emigration and death, measurement of reproductive success of a focal animal in a host (emigrated) group, need to be solved. However, conquering these difficulties, the increase of the number of long-term studied species may make it possible to collect effective data. I suppose that paternity identification with DNA finger-printing method (e.g., Inoue et al., 1991) will contribute to the problem. Secondly, it is necessary to clear up the inter-generation fluctuation patterns of N_e (Chepko-Sade & Shields, 1987). This can be reinterpreted in PT as to reveal the "population dynamics of reproductive groups."

Then, interrelation between the effective population and each functional group should be studied. Each functional group, i.e., feeding group, rearing group, etc., seems to have its own path through which it affects on individual fitness, and each path may affect each other. To study the evolutionary process of groupings, these paths should be cleared up and their effect-function on fitness should be decided. The function of each factor may differ among phylogenies and habitat conditions, although we have not got enough data to clear it up as yet.

The problem of interaction between each functional group is connected the second problem: membership stability. The groups of stable membership are called "social systems." Almost all non-human primate species have one or more group sizes in which memberships can be stable during a longer period of time. The factors for group forming, mentioned above, might not conclude such stableness. Group sizes would be affected by, say, anti-predation or pro-feeding-efficiency, or another factor, but stable membership can not lead to more benefit for the group members. The group sizes on which membership comes to be stable are different among species. In multi-level society species, such as geladas, stable membership is observed on more than one level. According to these, it is supposed that the traits of membership stableness has emerged as a consequence of interactions among group forming factors (cf. Dunbar, 1988). Some patterns of animal dispersions and kin relations can produce the same group for a given factor. If the animals possess a long-term memory and an ability for individual identification, it would be better for them to form a group with the same members. Some authors report the existence of reciprocal altruism in non-human primates (Packer, 1977; Seyfarth & Cheney, 1984). The benefit coming from the reciprocal altruism is in proportion to the number of animals in a group, with a certain number as a saturation level fixed by memory capacity and activity budget. The optimal value, single or plural, can be reduced from this benefit function and cost function of size change among different factors. That value may be equivalent with the stable membership size. To test this hypothesis, it is necessary to reveal the cost-benefit function of each functional group, the pattern of individual dispersion, and contribute function of each group on individual fitness.

I suppose, as seen above, that the groups in which membership is stable have emerged as a consequential trait from group forming shaped by selection on the size and composition. The reason is that the ability

for individual identification is more complicated and emerged later than that for recognition of group sizes. Therefore, the stability of group membership can not be discussed as a kind of group forming factor.

CONCLUDING REMARKS

I have reanalyzed the concept of group in the evolutionary studies, with materials of non-human primates. My conclusions are rather simple. First, the concept of group should be defined according to the aim of studies. Second, the current terminology for describing groups is not suitable for the study of evolution because it is based on the consequence of the group forming process and is greatly affected by the property of human perception. Third, when we consider the studies of evolution, groups should be defined according to the factors forming them. The reason is that none of the social system or the population is equivalent to the effective population. Furthermore, different factors, i.e., rearing, feeding, etc., could produce different structures of "groups."

The objects of discussion have been limited to non-human primates in this paper, but PT could be applied for non-primate animal species as well. That is why all groups of animals must have their function, as far as all animal species have social needs, at least to some extent. The pluralistic terminology could be applied to the problem of species individuality (Hull, 1976, 1978; Kitcher, 1984, 1989; Kawata, 1987, in press), but this problem needs another full-length paper.

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REFERENCES

- Andelman, S.: 1986, 'Ecological and social determinants of cercopithecine mating patterns', in D. I. Rubenstein and R.D. Wrangham (eds.), *Ecological Aspects of Social Evolution*. Princeton, NJ.: Princeton Univ. Press, pp.201-216.
- Anderson, C.M.: 1982, 'Baboons below the tropic Capricorn', *J. Hum. Evol.* 11, 205-217.
- Boesch, C. and H. Boesch: 1989, 'Hunting behavior of wild chimpanzees in the Tai National Park', *Am. J. Phys. Anthropol.* 78, 547-573.
- Brown, J.L.: 1983, 'Optimal group size in territorial animals', *J. Theoret. Biol.* 95, 793-810.
- Caldecott, J.O.: 1986, 'Mating patterns, societies and the ecogeography of macaques', *Anim. Behav.* 34, 208-220.
- Cheney, D.L. and R.M. Seyfarth: 1983, 'Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences', *Am. Nat.* 122, 392-412.
- Chepko-Sade, B.D. and D.S. Sade: 1979, 'Patterns of group splitting within materilinal kinship groups: a study of social group structure in *Macaca mulatta* (Cercopithecidae: Primates)', *Behav. Ecol. Sociobiol.* 5, 263-278.
- Chepko-Sade, B.D. and W.M. Shields, et al.:1987, 'The effects of dispersal and social structure on effective population size', in B.D. Chepko-Sade and Z.T. Halpin (eds.), *Mammalian Dispersal Patterns: The Effect of Social Structure on Population Genetics*, Univ. Chicago Press, Chicago, pp.287-321.
- Chism, J. and T.E. Rowell: 1986, 'Mating and residence patterns of male patas monkeys', *Ethology* 72, 31-39.
- Chivers, D.J.: 1974, *The Siamang in Malaya*, Karger, Basel.
- Churchland, P. M.: 1979, *Scientific Realism and the Plasticity of Mind*, Cambridge Univ. Press, Cambridge.

- Cords, M.: 1984, 'Mating patterns and social structure in redtail monkeys (*Cercopithecus ascanius*)', *Z. Tierpsychol.* **64** 313-329.
- Cords, M.: 1987, 'Forest guenons and patas-monkeys: male-male competition in one-male groups', in B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp. 98-111
- Dawkins, R.: 1982, *The Extended Phenotype*, Freeman, Oxford.
- de Ruiter, J.R.: 1986, 'The influence of group size on predator scanning and foraging behaviour of wedged capped capuchin monkeys (*Cebus olivaceus*)', *Behaviour* **98**, 240-258.
- Dittus, W.P.G.: 1984, 'Toque macaque food calls: semantic communication concerning food distribution in the environment', *Anim. Behav.* **32**, 470-477.
- Dittus, W.P.G.: 1986, 'Sex differences in fitness following a group take-over among toque macaques: testing models of social evolution', *Behav. Ecol. Sociobiol.* **19**, 257-266.
- Dunbar, R.I.M.: 1984, *Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies*, Princeton Univ. Press, Princeton.
- Dunbar, R.I.M.: 1987, 'Demography and reproduction', in B. B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.240-249.
- Dunbar, R.I.M.: 1988, *Primate Social Systems*, Kloom Helm.
- Dunbar, R.I.M.: 1989, 'Social systems as optimal strategy sets: the costs and benefits of sociality', in V. Standen and R.A. Foley (eds.), *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, Blackwell, Oxford, pp.131-149.
- Fossey, D.: 1983, *Gorillas in the Mist*, Houghton Mifflin, Boston.
- Fukuda, F.: 1983, 'Troop desertion by female Japanese macaques', *Jap. J. Ecol.* **33**, 347-355.
- Galdikas, B.M.F.: 1981, 'Orangutan reproduction in the wild', in C.E.

- Graham (ed.), *Reproductive Biology of the Great Apes*, Academic Press, New York.
- Gartlan, J.S. and T.T. Struhsaker: 1972, 'Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa', *J. Zool., Lond.* **168**, 221-266.
- Goldizen, A. W.: 1987, 'Tamarins and marmosets: communal care of offspring', in B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.34-43.
- Goodall, J.: 1968, 'The behaviour of free-living chimpanzees in the Gombe Stream area', *Anim. Behav. Monogr.* **1**, 161-311.
- Goodall, J.: 1986, *The Chimpanzees of Gombe: Patterns of Behavior*, Harvard Univ. Press, Cambridge, MA.
- Goosen, C.: 1981, 'On the function of allogrooming in Old-World monkeys', in A.B. Chiarelli and R.S. Corruccini (eds.), *Primate Behaviour and Sociobiology*, Berlin: Springer, pp.110-120.
- Hamilton, W.J., III, Buskirk, R. E. R. and Buskirk, W.H.: 1975, 'Chacma baboon tactics during intertroop encounters', *J. Mammal.* **56**, 857-870.
- Hamilton, W.J., III, Buskirk, R.E.R. and Buskirk, W.H.: 1976, 'Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp', *Ecology* **57**, 1264-1272.
- Hanson, N.R.: 1969, *Patterns of Discovery*, Cambridge Univ. Press, Cambridge.
- Hasegawa, T. and Hiraiwa, M.: 1980, 'Social interactions of orphans observed in a free-ranging troop of Japanese monkeys', *Folia Primatol.* **33**, 129-158.
- Hinde, R.A.: 1976, 'Interactions, relationships and social structure', *Man (ns)* **11**, 1-17.
- Hull, D.: 1976, 'Are species really individuals?' *Syst. Zool.* **25**, 174-191.
- Hull, D.: 1978, 'A matter of individuality', *Phi. Sci.* **45**, 335-360.

- Hull, D.: 1981, 'Units of evolution: a metaphysical essay', in U.J. Jensen and R. Harre (eds.), *The Philosophy of Evolution*, Harvester Press, Brighton, pp.23-44.
- Hutchins, M. and D.P. Barash: 1976, 'Grooming in primates: implications for its utilitarian function', *Primates* 17, 145-150.
- Inoue, M., A. Takenaka, S. Tanaka, R. Kominam and O. Takenaka: 1991, 'Paternity discrimination in a Japanese macaque group by DNA fingerprinting', *Primates*, 31, 563-570.
- Itani, J.: 1972, *Primate Social Structure*, Kyoritsu, Tokyo.
- Itani, J.: 1980, 'Social structure of African great apes', *J. Reprod. Fertil.*, Suppl. 28, 33-41.
- Itani, J.: 1985, 'The evolution of primate social structure', *Man (ns)* 20, 593-611.
- Janson, C.: 1985, 'Aggressive and individual consumption in wild brown capuchin monkey (*Cebus apella*). *Behav. Ecol. Sociobiol.* 18, 125-138.
- Kawai, M., R. Dunbar, H. Ohsawa and U. Mori: 1983, 'Social organization of gelada baboons: Social units and definitions', *Primates* 24, 1-13.
- Kawata, M.: 1987, 'Units and passages: A view for evolutionary biology and ecology', *Biol. Phil.* 2, 415-434.
- Kawata, M.: in press, *The Causes and Effects of Ecological and Evolutionary Processes*, SUNY Press, New York.
- Kitcher, P.: 1984, 'Species', *Phil. Sci.* 51, 308-333.
- Kitcher, P.: 1989, 'Some puzzles about species', in M. Ruse (ed.), *What the Philosophy of Biology Is: Essays Dedicated to David Hull*, Kluwer, Dordrecht, pp.183-208.
- Krebs, J.R. and N.B. Davies: 1987, *An Introduction to Behavioural Ecology*, 2nd edn, Blackwell, Oxford.
- Kudo, H.: 1987, 'The study of vocal communication of wild mandrills in Cameroon in relation to their social structure', *Primates* 28, 289-308.
- Kummer, H.: 1968, *Social Organization of Hamadryas Baboons*, Karger,

Basel.

- Kummer, H., A. Banaja, A. Abo-Khatawa and A. Ghandour: 1985, 'Differences in social behavior between Ethiopian and Arabian hamadryas baboons', *Folia Primatol.* **45**, 1-8.
- McKinnon, J.: 1974, 'The behaviour and ecology of wild orangutans (*Pongo pygmaeus*)', *Anim. Behav.* **22**, 3-74.
- Melnick, D.J. and M.C. Pearl: 1987, 'Cercopithecines in multimale groups: genetic diversity and population structure', in B. B. Smuts, D.L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.121-134.
- Mitani, J. C.: 1985, 'Mating behaviour of male orangutans in the Kutai Reserve, East Kalimantan, Indonesia', *Anim. Behav.* **33**, 392-402.
- Mitani, M.: 1991, 'Niche overlap and polyspecific associations among sympatric Cercopithecids in the Campo Animal Reserve, Southwestern Cameroon', *Primates* **32**, 137-151.
- Nishida, T.: 1968, 'The social group of wild chimpanzees in the Mahale Mountains', *Primates* **9**, 167-224.
- Nishida, T. and M. Hiraiwa-Hasegawa: 1987, 'Chimpanzees and bonobos: cooperative relationships among males', in B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.165-177.
- Nozawa, K.: 1991, 'Population-genetic studies of Japanese macaques: A review', *Primate Res.* **7**, 23-52.
- Oates, J. F.: 1977, 'The social life of a black-and-white colobus monkey, *Colobus gueraza*', *Z. Tierpsychol.* **45**, 1-60.
- Oi, T.: 1988, 'Sociological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island', *Primates* **29**, 1-19.
- Packer, C.: 1977, 'Reciprocal altruism in *Papio anubis*', *Nature* **265**,441-443.
- Popper, K. R.: 1959, *The Logic of Scientific Discovery*, Basic Books, New

York.

- Pusey, A.E. and C. Packer: 1987, 'Dispersal and philopatry', in B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.250-266.
- Ridley, M.: 1986, 'The number of males in a primate group', *Anim. Behav.* **34**, 1848-1858.
- Robinson, J. G. and C.H. Janson: 1987, 'Capuchins, squirrel monkeys, and atelines: socioecological convergence with Old World primates,' in B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.69-82.
- Rodman, P. S.: 1977, 'Feeding behaviour of orang-utans of the Kutai Reserve, East Kalimantan', in T. H. Clutton-Brock (ed.), *Primate Ecology*, Academic Press, London, pp.383-413.
- Rubenstein, D. I.: 1978, 'On predation, competition, and the advantages of group living', *Persp. Ethol.* **3**, 205-231.
- Rubenstein, D.I. and R.W. Wrangham (eds.): 1986, *Ecological Aspects of Social Evolution*, Princeton Univ. Press, Princeton, NJ.
- Sade, D.S., B.D. Chepko-Sade, M. Dow and J. Cheverud: 1987, 'Definition and measurement of migration in age-structured populations', in B. D. Chepko-Sade and Z.T. Halpin (eds.), *Mammalian Dispersal Patterns: The Effect of Social Structure on Population Genetics*, Univ. Chicago Press, Chicago, pp.225-247.
- Sakura, O.: 1991, 'On the concept of "group" in primates, with special reference to fission-fusion of chimpanzees', in A. Ehara, T. Kimura, O. Takenaka and M. Iwamoto (eds.), *Primate Today*, Elsevier, Amsterdam, pp.247-250.
- Sakura, O.: in prep, 'Factors affecting party size and composition of chimpanzees'
- Seyfarth, R.M. and D.L. Cheney: 1984, 'Grooming, alliances and reciprocal altruism in vervet monkeys', *Nature* **308**, 541-543.

- Sibly, R.M.: 1983, 'Optimal group size is unstable', *Anim. Behav.* 31, 947-948.
- Silk, J. B.: 1982, 'Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation', *Behaviour* 79, 162-188.
- Smuts, B.B.: 1985, *Sex and Friendship in Baboons*, Aldine, New York.
- Smuts, B. B., D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds): 1987, *Primate Societies* Chicago Univ. Press, Chicago.
- Stammach, E.: 1987, 'Desert, forest and montane baboons: multi-level societies', in B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T. T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.112-120
- Struhsaker, T. T.: 1967, 'Social structure among vervet monkeys (*Cercopithecus aethiops*)', *Behaviour* 29, 83-121.
- Struhsaker, T.T.: 1975, *The Red Colobus Monkey*, Univ. Chicago Press, Chicago.
- Sugiyama, Y.: 1968, 'Social organization of chimpanzees in the Budongo forest, Uganda', *Primates* 9 225-258.
- Sugiyama, Y.: 1976, 'Life history of male Japanese macaques', *Adv. Study Behav.* 7, 255-284.
- Sugiyama, Y.: 1990, *Ecological Reconsideration of Primate Social Structure*, Chuokoron, Tokyo.
- Symington, M.M.: 1988, 'Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*)', *Behaviour* 105, 117-134.
- Symington, M.M.: 1990, 'Fission-fusion social organization in *Ateles* and *Pan*', *Int. J. Primatol.* 11, 47-61.
- Takahata, Y.: 1982, 'Social relations between adult males and females of Japanese monkeys in the Arashiyama B troop', *Primates* 23, 1-23.
- Terborgh, J.: 1983, *Five New World Primates*, Princeton Univ. Press, Princeton, NJ.

- Tsingalia, H.M. and T.E. Rowell: 1984 'The behaviour of adult male blue monkeys', *Z. Tierpsychol.* **64** 253-268.
- van Schaik, C.P.: 1983, 'Why are diurnal primates living in groups?' *Behaviour* **87**, 120-144.
- van Schaik, C.P. and M.A. Noordwijk: 1985, 'The evolutionary effect of the absence of felids on the social organization of the Simeulue monkey (*Macaca fascicularis fusca*, Miller 1903)', *Int. J. Primatol.* **6**, 180-200.
- van Schaik, C.P., M.A. van Noordwijk, M.A. Wasone and E. Sitriono: 1983, 'Party size and early detection in Sumatran forest primates', *Primates* **24**, 211-221.
- Warburton, K. and J. Lazurus: 1991, 'Tendency-distance models of social cohesion in animal groups', *J. Theor. Biol.* **150**, 473-488.
- Watanabe, S.: 1969, *Knowing and Guessing*, John Wiley & Sons.
- Watanabe, S.: 1985, *Pattern Recognition: Human and Mechanical*, John Wiley & Sons.
- Wilson, D.S.: 1983, 'The group selection controversy: history and current status', *Ann. Rev. Ecol. Syst.* **14**, 159-187.
- Wilson, E.O.: 1975, *Sociobiology: The New Synthesis*, Harvard Univ. Press, Cambridge, MA.
- Wrangham, R.W.: 1977, 'Behaviour of feeding chimpanzees in the Gombe National Park, Tanzania', in T.H. Clutton-Brock (ed.), *Primate Ecology*, Academic Press, London, pp.503-538.
- Wrangham, R.W.: 1981, 'Drinking competition in vervet monkeys', *Anim. Behav.* **29**, 904-910.
- Wrangham, R.W.: 1983, 'Ultimate factors determining social structure', in R. A. Hinde (ed.), *Primate Social Relationships*, Blackwell, Oxford, pp.255-262.
- Wrangham, R.W.: 1987, 'Evolution of social structure', in B.B. Smuts, D.L. Cheney, R. M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.), *Primate Societies*, Univ. Chicago Press, Chicago, pp.282-296.

- Wrangham, R.W. and Rubenstein, D.I.: 1986, 'Social evolution in birds and mammals', in D.I. Rubenstein and R.W. Wrangham (eds.), *Ecological Aspects of Social Evolution*, Princeton Univ. Press, Princeton, NJ, pp.452-470.
- Wrangham, R.W. and B.B. Smuts: 1980, 'Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania', *J. Reprod. Fertil. Suppl.* 28, 13-31.
- Yamagiwa, J.: 1987, 'Male life history and the social structure of wild mountain gorillas (*Gorilla gorilla beringei*)', in S. Kawano, J.H. Connell and T. Hidaka (eds.), *Evolution and Coadaptation in Biotic Communities*, Univ. Tokyo Press, Tokyo, pp.31-51.

Table 1. Some examples of terms describing non-human primate groups.

Species	Terms describing groups			Sources
	Group size			
	small ←		→ large	
Gelada	one-male unit	band	herd	Kawai et al. (1983)
Hamadryas	one-male unit	clan	band troop	Kummer (1968)
Vervet		troop	community	Cheney & Seyfarth (1983)
Macaque		group (troop)		-----
Ateles		subgroup	group	Robinson & Janson (1987)
Chimpanzees		party	community	Goodall (1986)
		(subgroup)	(unit-group)	Nishida & Hiraiwa-Hasegawa (1987)
Gorilla		Group	Community	Fossey (1983)

For almost all species, term of "coalition" refers to the highest affiliations (smallest group), and "population" refers to the lowest affiliation (largest group).

Table 2. Factors affecting group formation and the characteristics of their fitness function

Factors	Type of function	Party size on which individual fitness gets the maximum value
anti-predation	convex up	large
resource defense	convex up	medium - large
anti-disease	Gaussian curve	small - medium
rearing efficiency	convex up or Gaussian curve	small
feeding efficiency	Gaussian curve or concave up	small?
copulation success	Gaussian curve	small - medium

FIGURE LEGENDS

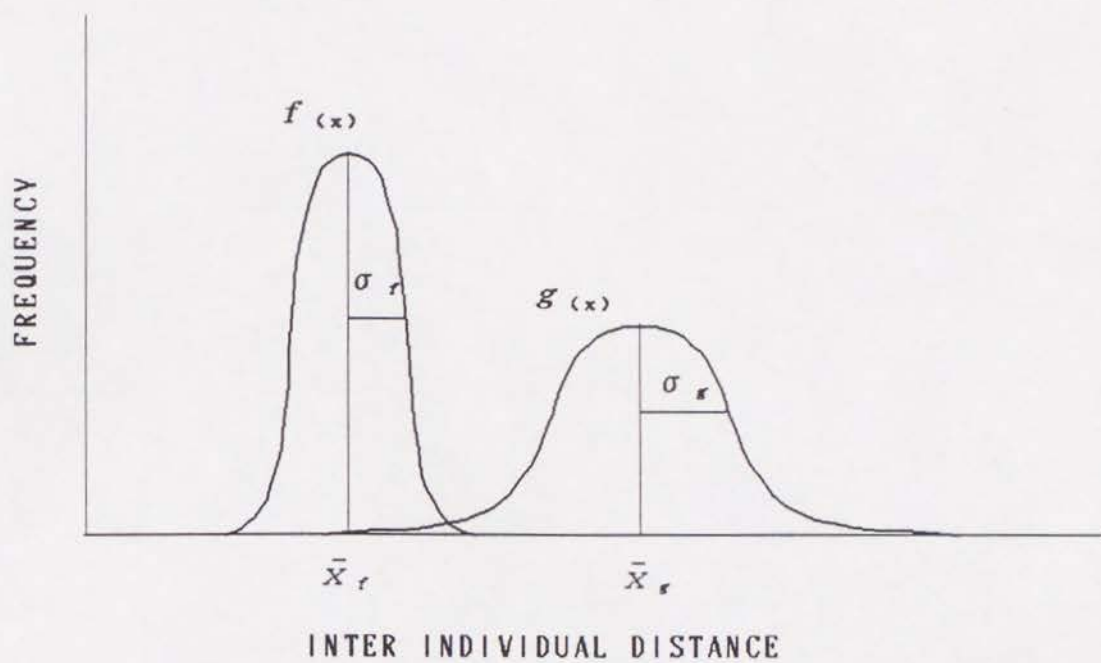
Figure 1. The definition of the disuniformity of inter-individual distances (IID), or spatial-distribution of animals. When a function has smaller mean and smaller variance than the other one, the distribution of IIDs represented by the function is defined as "disuniform," and the set of individuals belonging to the range of the variable of the function is defined as "group."

Figure 2. Schemes of the pattern of spatial-distribution of individuals. Each small closed circle represent a individual. (a) uniform, (b) random, (c) disuniform distribution. Observers will recognize "groups" as circled by dotted lines.

Figure 3. Frequency of approach of non-troop males to a troop of Japanese macaques (*Macaca fuscata*). The frequency was represented by the ratio of attendance at the feeding-ground. Open bars: "troop" males; hatched bars: "non-troop" males. The ratio declined gradually among non-troop males. The data were collected during a 1984-85 copulatory season of Shiga A₁ troop, in Nagano Prefecture, central part of Honshu Island, Japan.

Figure 4. A schema of groups classified pluralistically according to their function. The largest rectangle represents a "troop," or, a social group. Rectangles of different shades represent groups for different function: e.g., groups for feeding, for breeding, for rearing, etc. Such groups are not closed within a social group, and can even be formed with animals of different species.

Fig. 1



F i g . 2

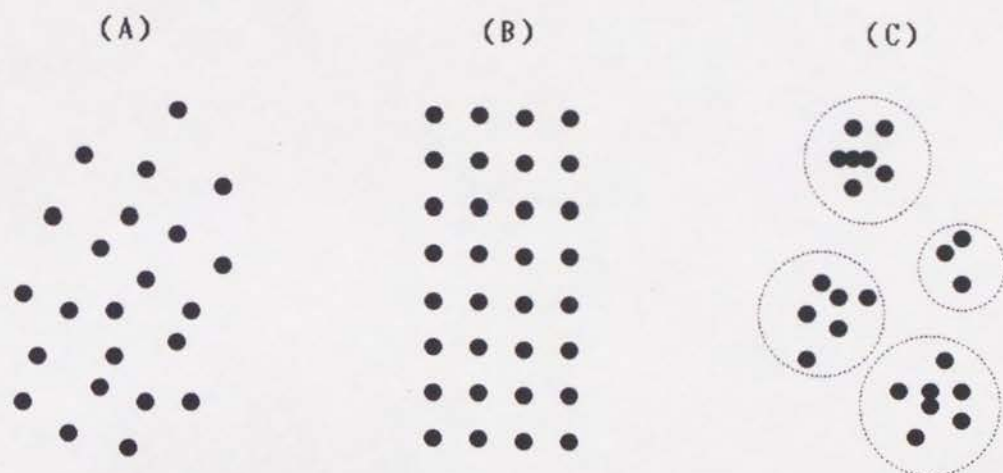
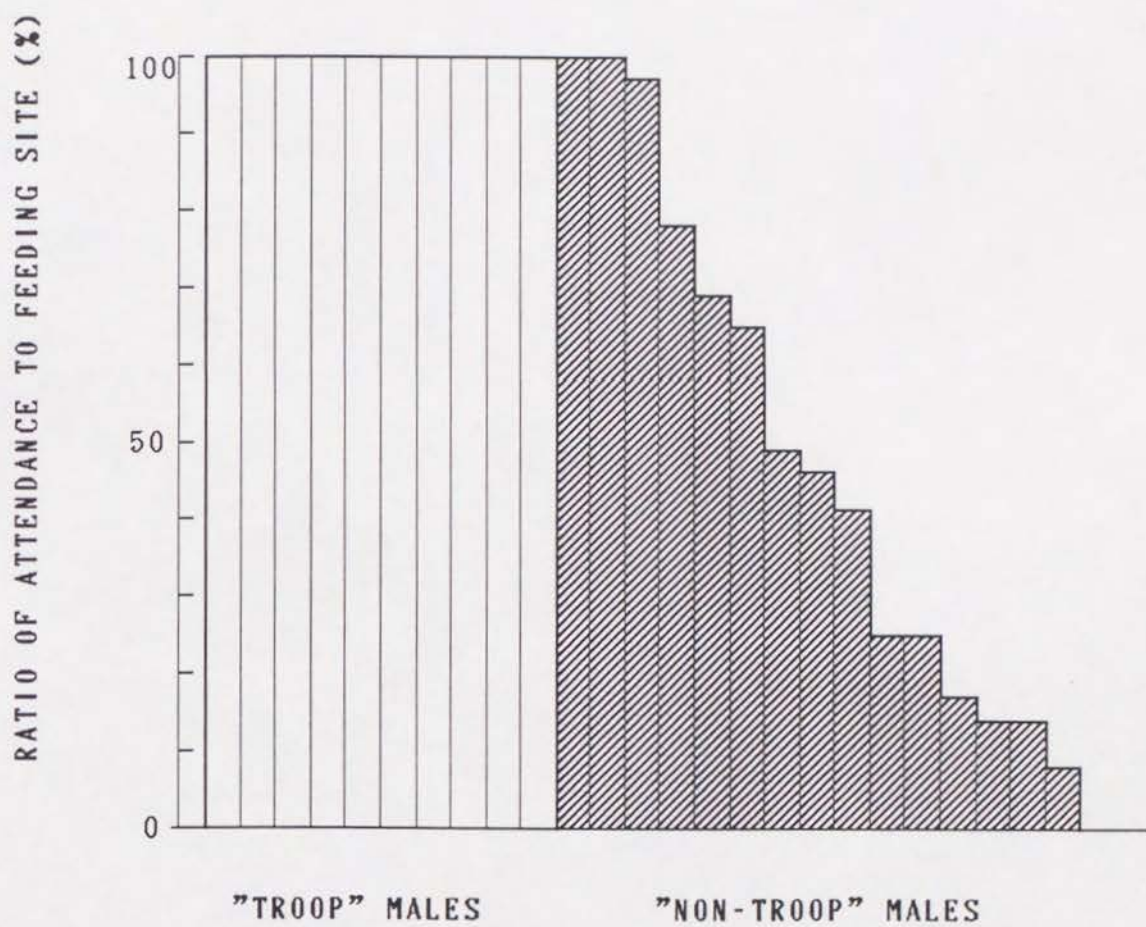
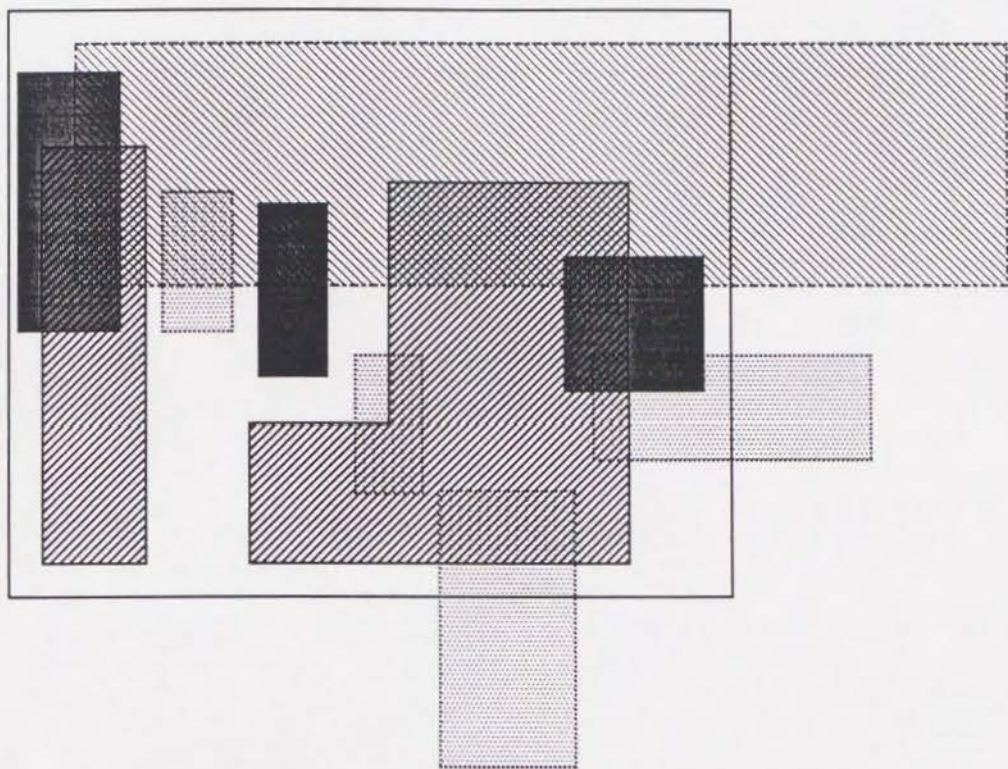


Fig. 3



F i g . 4



FACTORS AFFECTING PARTY SIZE AND COMPOSITION OF CHIMPANZEES

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JAPAN

SUMMARY

The party sizes of western chimpanzees (*Pan troglodytes verus*) and assumed factors affecting them were studied in Bossou, Republic of Guinea, West Africa. Party sizes and feeding ratio were negatively correlated, and larger parties tended to be formed in more dangerous situations (i.e., crossing roads with much traffic). When parties included estrous females young (i.e., more than late adolescence) males tended to forage with the estrous females, independent from the mother. Lactating females with an infant had a tendency to spend more time alone, but the trend was not so apparent as in *P. t. scweinfurthii* in Gombe, Tanzania. These facts suggest that several factors, not only foraging, affected party formation, or fission-fusion, of chimpanzees. It seems that classification of groups according to their factors will present a more standard point of view.

Key Words: *Pan troglodytes verus*, party size, party composition, feeding and other factors

INTRODUCTION

Many animal species are living in groups. There are supposedly many kinds of evolutionary ultimate factors affecting group formation: anti-predation, resource defense, feeding efficiency, copulatory success, caring for the young, anti-disease, and so forth (see Rubenstein & Wrangham, 1986; Krebs & Davies, 1987; Dunbar, 1988 for reviews). The optimal group size for each factor usually differs among factors. This supports the point of view that animals do not form groups organized as one system, but form them by corresponding to each factor and adjusting their size and composition (Dunbar, 1989; Sakura, 1991, in prep). In other words, the structure of animal groups is not a fixed one, but fluctuates according to circumstance, in both the microscopic and macroscopic worlds. This pluralistic model of groups have two advantages: first, it is easier to describe variable group formation patterns; and second, functional analysis through comparative method is simpler (Sakura, in prep). The aim of this paper is to apply the model to chimpanzees, focused on the first advantage.

The social systems of common chimpanzees (*Pan troglodytes*) are characterized by its fission-fusion pattern (Goodall, 1968; Nishida, 1968; Sugiyama, 1968; Wrangham, 1975). They forage forming temporal small parties (or sub-groups) whose members come from a larger community (or unit-group) of stable membership. Since this characteristic has been observed, more or less, in all populations of chimps which have been studied until now, it must be a common social system within the chimpanzee (see Sugiyama, 1973; Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987 for reviews). Group composition produced by such a pattern may reflect the effect of some factors of group formation, and it enables researchers to carry out the functional analysis.

In general, fission-fusion party formation has been regarded as the strategy for decreasing feeding competition. To support this, the

following facts have been observed. First, chimps change their party size according to the size and quality of feeding patches (Wrangham, 1975, 1977; Ghiglieri, 1984; Goodall, 1986; Isabirye-Basuta, 1988; White & Wrangham, 1988); Second, larger parties are formed in hunting situations (Boesch & Boesch, 1989). However, food distribution is not the only determinant of party size. Estrous females attract males and produce larger parties (Riss & Busse, 1977; Tutin, 1979; Goodall, 1986), and lactating females tend to spend more time alone (Wrangham & Smuts, 1980). They seem to be more gregarious in open spaces like the savanna (cf. Itani & Suzuki, 1967), and party sizes come to be larger during movement (Tutin et al., 1983).

Therefore, party composition of chimpanzees is affected by various factors and it is not reasonable to limit the context merely to feeding efficiency. Goodall (1986) summarizes factors affecting party size and composition as follows: 1) food supply; 2) presence of danger; 3) estrous females; 4) presence of infants. In this paper, investigating each of these factors in turn, I will report the relation between size, composition and behavior displayed by the group of chimpanzees.

MATERIALS AND METHOD

Objects

The objects of the study were habituated western chimpanzees (*P. t. verus*) in Bossou, Guinea, West Africa. They have been studied by Sugiyama and his colleagues since 1976, thus, the degree of habituation and data on kin relation and individual identification were sufficient (see Sugiyama, 1989 for a recent review). Many parts of their ranging area of 8 or 10 km² were covered by the secondary forest, cultivated fields, and only some areas of primary forest. Annual rain fall is estimated ca.3000mm (see Sugiyama & Koman, 1979, 1987; Kortlandt, 1987 for detailed description of habitat). My study was carried out from September 1987

to March 1988 (Period I) and from November 1989 to March 1990 (Period II), ten months total.

Throughout my study, the community size was around 20, including infants. We had just one fully matured male. The number of adolescent males had been four at the beginning of the Period I, and then three because one died during the Period (Matsuzawa et al., 1990). One of the three had disappeared until the beginning of the Period II, which left just two. Age-sex composition of the community is summarized on Table 1. The age stage was divided every four years according to the population dynamics of the Bossou community (Sugiyama & Koman, 1979; Sugiyama, 1981, 1984, 1989). "Cycling females" were defined as the females whose offspring was more than equal 4yrs-old, or whose sexual swelling was observed during the study periods. "Lactating females" were the females whose offspring was less than 4yrs-old and sexual swelling was not observed. During Period II, *Pm* and *Ki* showed sexual swelling regularly, although both of them had an infant aged two or three yrs old, so they were regarded to be in "cycling."

We artificially fed chimpanzees during the second study period for experimental studies on tool use behavior (Fushimi et al., 1991, see also Sakura & Matsuzawa, 1991). We fixed 20 or 30 pieces of bananas a day at a feeding ground where was naturally a rather open space in the forest. The chimps visited the feeding ground one time per three or four days, and usually spent less than one hour with the maximum of two hours. I estimated that the effect of artificial feeding on their grouping formation was negligible, so that the data collected during Period II was not eliminated. However, party composition observed in the feeding ground was discarded.

Sampling methods

Data on party composition and size was collected by the one-zero

sampling method (Altmann, 1974) of which the unit is one day. If I observed that chimp A joined a party including chimps B, C and D, two parties were recorded. After that, if D left the party of ABC, only one time was recorded for parties ABC and D, as far as the events occurred within a same day. I eliminated the data of parties observed less than 30 min. The reason of the use of the unit "one day" is that the preceding studies in Gombe and Mahale revealed that the duration of same parties are not frequently over the range from few hours to few days (Wrangham, 1975; Nishida, 1979).

Activity of individuals was collected with 10min scan-sampling method (Altmann, 1974), because the observation condition were too tough to use focal animal sampling. The ten minute interval was decided after White & Wrangham (1988).

Even after the artificial feeding mentioned above, the observation of the chimps on ground was usually difficult, and almost impossible in the area of the secondary forest because of the dense bush. Thus, data collection was biased in the cases in which chimps were in the trees.

Definition of terms

In this paper, "party" is defined as individuals within a 30m radius because of the following reasons: First, Sugiyama & Koman (1979) who have been carrying out the preceding studies in Bossou accept this criterion. They call, however, the individuals within a 30m radius a "compact association," distinguished from their "party" as individuals within a 200m radius. Thus, "party" in this paper is associated with "compact association" of Sugiyama & Koman (1979). The second reason came from the observation conditions. As mentioned above, it was difficult on the ground to confirm all animals over 30m radius. In the trees, animals within 30m radius were easily identified, sometimes even 100m was possible. Therefore, the criterion of less than 30m would be

hard to apply to arboreal conditions, and that of more than 30m would bias the data in terrestrial conditions. Thus the reason for the 30m criterion.

"Party size" in this paper means the number of independent animals in a party. "Independent animals" were operationally defined as the chimps whose likelihood of independent foraging, i.e., foraging in a party different from their mother's, was more than 0.67. However, the females with offspring were considered as independent animals, regardless of the likelihood of their independence from the mother. The maximum score of the party size was nine throughout the periods. When I mention the party composition in the following section, premature animals are also regarded as party members.

RESULT

Distribution of party sizes

The frequency distribution of directly observed party sizes might be biased to larger groups. To investigate the bias, the relation between the numbers of observers and the party sizes is shown in Fig. 1. There were one (myself) or two observers during Period I (1987-88), and three or four (including myself) during Period II (1989-90). The party size distribution of each period did not differ significantly (Kolmogorov-Smilnov two sample test, $D=0.094$, $P>0.05$, two-tailed). This suggested that the bias from observation conditions, or the number of observers, was negligible. From this result, the data from Period I and II is combined in the following sections, unless otherwise indicated.

Fig. 2 represents the monthly fluctuation of mean party sizes. The party size increased after the end of a dry season, and in the early part of the rainy season. This tendency was similar in both study periods, although the mean sizes for November and December in Period II showed smaller values than those in Period I.

Feeding and party size

It is predicted that party sizes and time spent on feeding correlate negatively because of inter-individual feeding competition. Very large feeding patches, however, offer superabundant food supply, and, thus, may eliminate the effect of feeding competition. Here, analyzing the data of only arboreal parties, I investigated the relation between party size and the feeding ratio of a party. The feeding ratio of a party (Rf) was defined as follows:

$$\text{Rf} = \frac{\text{No. of total scanned feeding animals of a focal party}}{\text{No. of total scanned animals of the party.}}$$

Fig. 3 shows the effect of Rf on party size. Mean party size of which Rf was more than equal 0.5 was 3.6 ($SD=1.849$, median=3, $N=34$), while it was 5.7 ($SD=2.702$, median=6, $N=37$) for that Rf was less than 0.5. The former was significantly greater than the latter (Mann-Whitney U -test, $Z=3.35$, $P<0.01$). Furthermore, the party sizes negatively correlated with Rf ($r_s=-0.294$, $P<0.05$, $N=71$), the Bossou chimpanzees in smaller parties spent more time in feeding.

The low correlation between party size and Rf might be caused from the disregard of patch size (cf. White & Wrangham, 1988). However, neither measure of patch size (DBH, canopy diameter) nor patch quality (chimp-minutes for feeding; White & Wrangham, 1988) correlated with party size (Sakura et al., 1991). Table 2 shows the example, comparison between a fig tree (*Ficus mucoso*) and *Antiaris africana*. Both trees had a similar patch size, DBH more than 150cm and more than 30 chimp-minutes, but mean party size was 4.1 on the fig tree and 1.4 on the *Antiaris*.

Estrous females and party composition

In the Bossou community, the presence of estrous females could not change party size (by my definition) because we had just one

sexually full matured male throughout the periods. However, the behavior of young males was affected. I consider the dependent males in late juveniles (7yrs-old) and in adolescence (9-10yrs-old) as the "young males" in this section, and will investigate the effect of the presence of estrous females on their behavior and party composition. The data collected during Period I and II are analyzed separately here, because the number of young males and cycling females differed among the two periods (Table 1).

A young male was able to ejaculate and his copulation with an adult estrous female was often observed. When maximal tumescence was synchronized among a few females, one of them ignored by the adult male even showed courtship display for the young male. However, the semination ability of young males is unknown.

First, the ratio of parties including young and adult males was compared among sexual parties (including at least one estrous females) and non-sexual ones (including no estrous female) (Table 3). During Period I, the ratio of parties including males was 96% in sexual parties, while the ratio decreased to 62% in non-sexual parties ($\chi^2=21.51$, $P<0.01$, $df=1$). This tendency was similar in Period II, the ratio was 93% in sexual parties, while 54% in non-sexual ($\chi^2=47.23$, $P<0.001$, $df=1$). Thus, males tended to exist in the same party including estrous females.

Second, the ratio of young-male-independent parties in which young, independent, males foraged without their mother, was compared among sexual and non-sexual parties (Table 3). That ratio was 33.3% (Period I) and 39.5% (Period II) in sexual parties, while it decreased to 7.5% (Period I) and 27.6% (Period II) in non-sexual parties (Period I: $\chi^2=16.12$, $P<0.001$, $df=1$; Period II: $\chi^2=4.11$, $P<0.05$, $df=1$). Thus, the presence of estrous females stimulated the independent foraging of young males. It should be mentioned that the degree of independent foraging of young males was higher in Period II, whether estrous females existed

or not. This might be caused by the age of the focal young males. In Period I, we had two or three males at age seven years and one at nine years, while two nine years old males were in Period II (Table 1; see above).

Thirdly, I compared the socioeconomic sex ratio (no. of males / no. of females) within each party among sexual and non-sexual parties (Table 3). In Period I, mean SSR was 0.81 for sexual parties, while 0.45 for non-sexual parties; estrous females caused more cohesive distribution of males (Kolmogorof-Smirnov test, $D=0.314$, $P<0.001$, two-tailed). This was also the case in Period II, the mean SSR was 0.60 for sexual parties, while 0.35 for non-sexual ones ($D=0.497$, $P<0.001$). Both score of the SSR were lower in Period II, might have caused the difference of the number of young males.

Presence of danger and party size

Next, I investigated the effect of the presence of danger on the party sizes. The roads of seven meter width cross over the ranging area of the Bossou chimps, which lead to the Guinea-Liberian border. On the roads there were 20 or 30 car accidents per day as well as much local traffic. Seeing the chimpanzees, the local people often reacted in fear to them and ran around loudly shouting, although they did no harm to the chimps. So that, the chimps tended to avoid them. The Bossou chimpanzees crossed over the roads one time per every two or three days. It seemed quite a strained situation for them to cross the roads, because of the openness and heavy traffic.

When they crossed the roads, the first party often waited for a chance in the bush beside the road until the second coming party joined them, and then they would start to cross after that. The chimps in the first party sometimes pant-hooted in such a situation, and the second party responded to it by joining them. Therefore, it can be predicted

that the party size is larger in the situations of crossing over the roads than in others. Fig. 4 shows the result of the comparison of sizes of parties which crossed over the roads and of those which moved in the forests. The latter included the parties of which the ratio of feeding and resting was less than 10%. It was rather difficult to identify all members of a moving party on the ground in the forests, because of poor visibility. It was easier to confirm membership in a party crossing over the roads. The mean size of parties crossing a road was 5.8 individuals ($SD=3.16$, median=7, $N=49$), and that of parties moving in forests was 4.5 ($SD=2.38$, median=4, $N=47$). The former is significantly larger than the latter (Mann-Whitney U -test, $z=2.25$, $P<0.05$, two-tailed). The ratio of the parties which include the alpha male also differ: 66% for crossing a road and 48% for moving in the forests ($\chi^2=4.11$, $P<0.05$, $df=1$). The chimpanzees formed significantly larger parties with the alpha male in more dangerous conditions, such as crossing roads.

Concerning the observation conditions, the difference may be more larger. First, because the observation conditions were better on the roads than in the forests; Second, because we tended to catch up to a party crossing the roads. When we could not find the chimps in the forests, sometimes we waited for them on the roads. Thus, our observation for the chimpanzees crossing the roads was closer to point observation, while the larger parties could be easily observed in forests. This would magnify the difference reported here.

The presence of infants and party size

Next, I compared the party formation patterns among lactating females and cycling females. A lactating female often foraged alone, only with her offspring, and sometimes apparently avoided a sexual party including the adult male and estrous females. In other cases, however, she foraged in a party with other lactating females, it could not be

concluded that a lactating female tended to spend more time alone.

As mentioned above, I could not use focal animal sampling and therefore the time budget in which a female foraged alone could not be calculated. If it had, the data would be very biased. Then, I used an index of affinity based upon the frequency in which a chimp formed the same party with another. The affinity index (d_{AB}) among chimp A and B is defined as:

$$d_{AB} = n(A \cap B) / (n(A) + n(B) - 2n(A \cap B))$$

where $n(A)$ represents a frequency of a party including A, $n(A \cap B)$ that of a party including both A and B.

Fig. 5 shows a dendrogram of affinity among females, calculated from the index. The Ward method was used for the cluster analysis. Fig. 5 (A) is for Period I, and (B) for Period II. Two dendrograms show a similar tendency with some difference. In Period I, lactating females (*Pm*, *VI*, *Nn*), except a mother-daughter pair (*Ka* and *Ki*), tended to show a lower degree of affinity than females having no infants. In Period II, however, such a tendency was not so clear: *Jr*, a lactating one, had a rather high degree of affinity, and cycling *VI*, *Nn* and *Pm* made their own cluster. Thus, these dendrograms seemed to reflect the affinity patterns based on individual specific characters, and not on sexual characteristics (i.e., cycling or lactating) of females.

To confirm this in detail, the ratio of a female foraging in the same party with the sexually full matured male (*TA*) was compared among the periods (Fig. 6). Six females had different sexual stages during the two periods. Four of six (*Nn*, *Jr*, *VI*, *Yo*) showed higher ratios in the cycling state than in the lactating state, which confirms the prediction. The other two, *Pm* and *Ki*, however, foraged more in the same party with *TA* in the lactating state than in the cycling state. Thus, in Bossou, it could not be concluded that the cycling females tended to forage more with the sexually matured male ($P > 0.2$, binomial test). The change of the

ratio should be noticed in females who were in the cycling states in both periods, *Ka* and *Fn*. *Ka* shared the same party with *TA* more than *Fn* in Period I, while *Fn* foraged with *TA* more than *Ka* in Period II.

From these, it is suggested for the Bossou chimps that there is a group of females (*Ka*, *Ki*, *Jr*) which shows a higher affinity with the adult male (*TA*), and the other females (*Vl*, *Nn*, *Yo*) tend to be rather solitary. *Fn* and *Pm* may be located between the two groups. Affiliative relations among females seem to be framed by such characteristics, and the female sexual state may effect the individual relationship within the framework.

DISCUSSION

This study revealed that several factors affect the composition of chimpanzee parties. The first factor is feeding: chimpanzees tended to form a smaller party for feeding. The effect of the feeding patch size and the quality has not been clear, but a similar tendency has been observed in the chimpanzees in Gombe (Wrangham, 1975, 1977) and Kibale (Isabirye-Basuta, 1988).

Second, the presence of estrous females caused more cohesive distribution among the males. The young males who usually forage in the same party with their mother tended to join a party including estrous females. The preceding studies in Gombe (Riss & Busse, 1977; Tutin, 1979; Wrangham & Smuts, 1980; Goodall, 1986) and in Mahale (Nishida, 1979; Hasegawa & Hiraiwa, 1983) have reported the similar phenomena.

Third, the chimps in Bossou formed a larger party in the more dangerous situation. The clear evidence for the effect of the presence of danger has not been reported, without some suggestive facts (Itani & Suzuki, 1967; Tutin et al., 1983). Some authors champion the anti-predation hypothesis as a main factor for forming a large group (Alexander, 1974; van Schaik, 1983; Dunbar, 1988), which is supported by the result presented here.

Fourth, the parties showed seasonal fluctuation: larger in the early dry season than in the rainy season. This tendency has also been confirmed in Mahale (Nishida, 1968, 1979) and Gombe (Wrangham, 1975, 1977). The food supply might cause the seasonal fluctuation (Wrangham, 1975; Nishida, 1979), although we have not collected enough data on this in Bossou.

The fifth factor concerns the presence of infants. In Gombe this factor has much more effect on female party formation (Wrangham & Smuts, 1980; Goodall, 1986). In Mahale, however, this has not been so apparent as in Gombe (Uehara, 1981; Kawanaka, 1984; Hasegawa, 1990). In Bossou, like in Mahale, the presence of the infant affected the party formation, but the effect was not so clear. I think this is caused by the fact that the chimps of Bossou tend to form more cohesive groups (Sugiyama & Koman, 1979) and that inter-female relationships are highly affiliative as well as male-female relationships (Sugiyama, 1988). A community size in Bossou is not large and the number of adult males is small (just one during the study periods) and infanticide has not been observed in Bossou. This suggests that a rearing female may not need to avoid an adult male. Furthermore, the low rate of female dispersion (Sugiyama, 1981, 1984, 1989) may allow cooperative rearing among females. Matsuzawa & Sakura (unpublished data) observed a female crossing over a road who handed her infant to another female whose kin relation was less than at least 0.25. If such altruistic relations can be expected to be common, a lactating female need not forage alone.

As we have seen, a given party must be affected by one or more factors. Thus I believe that the fission-fusion society can be described by the pluralistic model (see Introduction and Sakura, in prep). Furthermore, the term "party" may not be an adequate one for describing chimpanzee grouping patterns. The concept of "party" and "community" deal only with manifestations of the cohesion of animals rather than

mechanisms for cohesion. A concept dealing with this mechanism is necessary to functional analysis, because contributions of the fitness of individual animals forming groups are different among the different functions of the groups, i.e., breeding, feeding, rearing (cf. Kawata, in press. see Sakura, in prep, for my alternative).

Another advantage of the pluralistic model is that it will make inter-specific comparison easier. Although this study cannot present direct perspectives on that point, the comparison with bonobos (*P. paniscus*) can be carried out as follows. Bonobos, a neighboring species of chimps, tend to form a larger "party" than chimps (Wrangham, 1986; Nishida & Hiraiwa-Hasegawa, 1987). Wrangham (1986) attributed this phenomena to the fact that bonobos consume terrestrial herbs more than chimps do. Terrestrial plants supply larger food patches than arboreal ones and this should allow a less competitive situation in a feeding party. Then, as a consequence, the party size of bonobos could become larger. The pluralistic model predicts other effects, e.g., sexuality, which may also cause the difference. The ratio of sexual, or mixed, party is higher in bonobos than in chimps (Kuroda, 1979; Kano, 1982; Badrian & Badrian, 1984). More than 95% of the parties of bonobos in Wamba are sexual parties (Kano, 1982, 1987), while the ratios were 37% (Period I) and 48% (Period II) for the chimps in Bossou. The figures in Bossou point within the range of the ratios in the chimps from other areas (38-78%, $N=7$. Tutin et al., 1983; Nishida & Hiraiwa-Hasegawa, 1987). Thus they seem to be standard values concerning the ratio of sexual parties in common chimps. The high ratio of sexual parties in bonobos may be attributed to the elongated sexual swelling period of bonobo females (Furuichi, 1987). This may cause larger parties in bonobos.

The mean size of sexual parties of common chimps was 5.2 ($SD=1.14$, $N=178$) in Bossou. This figure is similar to those of bonobos in Lomaco (4.33, 7.15, 9.69 for three communities; White, 1989). The bonobos

in Wamba form larger sexual parties in which the mean size is 14 (N=172, including three non-sexual parties; Kano, 1987), which maybe have been caused by its larger community size. Party formation in bonobos is also affected by the other factors mentioned in this study (White, 1988, 1989), thus the comparison of sexual party size among the two species has its grounds. From this, it is suggested that the elongated estrous period of bonobo females causes larger parties, although a more systematic comparison is necessary to confirm this hypothesis.

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REFERENCES

- Alexander, R.D. (1974). The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 5: 325-383.
- Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* 49: 227-267.
- Badrian, A. and Badrian, N. (1984). Social organization of *Pan paniscus* in the Lomaco Forest, Zaire. In: Sussman, R.L. (ed.), *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*, Plenum Press, New York.
- Boesch, C. and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *Am. J. Phys. Anthropol.* 78: 547-573.
- Dunbar, R.I.M. (1988). *Primate Social Systems*, Croom Helm, London.
- Dunbar, R.I.M. (1989). Social systems as optimal strategy sets: the costs and benefits of sociality. In: Standen, V., and Foley, R.A. (eds.), *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, Blackwell, Oxford, pp.131-149.
- Furuichi, T. (1987). Sexual swelling, receptivity and grouping of wild pygmy chimpanzee females at Wamba, Zaire. *Primates* 26: 219-237.
- Fushimi, T., Sakura, O., Matsuzawa, T., Ohno, H. and Sugiyama, Y. (1991). Nut-cracking behavior of wild chimpanzees (*Pan troglodytes*) in Bossou, Guinea (West Africa). In: Ehara, A., Kimura, T., Takenaka, O., and Iwamoto, M. (eds.), *Primate Today*, Elsevier, Amsterdam, pp.695-696.
- Ghiglieri, M.P. (1984). *The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure*, Columbia Univ. Press, New York.
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream area. *Anim. Behav. Monogr.* 1: 161-311.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*, Harvard Univ. Press, Cambridge, MA.
- Hasegawa, T. (1990). Sex differences in ranging patterns. In: Nishida, T.

- (ed.), *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, Univ. of Tokyo Press, Tokyo, pp.99-114.
- Hasegawa, T. and Hiraiwa-Hasegawa, M. (1983). Opportunistic and restrictive matings among wild chimpanzees in the Mahali Mountains, Tanzania. *J. Ethol.* 1: 75-85.
- Isabirye-Basuta, G. (1988). Food competition among individuals in a free-ranging chimpanzee community in Kibale Forest, Uganda. *Behaviour* 105: 135-149.
- Itani, J. and Suzuki, A. (1967). The social unit of chimpanzees. *Primates* 8: 355-381.
- Kano, T. (1982). The social group of pygmy chimpanzees (*Pan paniscus*). *Primates* 23: 171-188.
- Kano, T. (1986). *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*, Princeton Univ. Press, Princeton, NJ (tr. into English by E. Ono-Vineberg).
- Kawanaka, K. (1984). Association, ranging, and the social unit in chimpanzees of the Mahali Mountains, Tanzania. *Intl. J. Primatol.* 5: 411-434.
- Kawata, M. (in press). *The Causes and Effects of Ecological and Evolutionary Processes*, State Univ. of New York Press, New York.
- Kortlandt, A. (1986). The use of stone tools by wild-living chimpanzees and earliest hominids. *J. Hum. Evol.* 15: 77-132.
- Krebs, J.R. and Davies, N.B. (1987). *An Introduction to Behavioural Ecology*, 2nd edn, Blackwell, Oxford.
- Kuroda, S. (1979). Grouping of the pygmy chimpanzees. *Primates* 20: 161-183.
- Matsuzawa, T., Sakura, O., Kimura, T., Hamada, Y. and Sugiyama, Y. (1990). Case report on the death of a wild chimpanzee (*Pan troglodytes verus*). *Primates* 31: 635-641.
- Mitani, M. (1991). Niche overlap and polyspecific associations among

- sympatric Cercopithecids in the Campo Animal Reserve, Southwestern Cameroon. *Primates* 32: 137-151.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9: 167-224.
- Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In: Hamburg, D.A. and McCown, E. (eds.), *Great Apes*, Benjamin/Cummings, Menlo Park, CA. pp.72-121.
- Nishida, T. and Hiraiwa-Hasegawa, M. (1987). Chimpanzees and bonobos: cooperative relationships among males. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.D., Wrangham, R.W. and Struhsaker, T.T. (eds.), *Primate Societies*, Chicago Univ. Press, Chicago, pp.165-180.
- Riss, D.C. and Busse, C.D. (1977). Fifty-day observations of a free-ranging adult male chimpanzee. *Folia Primatol.* 28: 283-297.
- Rubenstein, D.I. and Wrangham, R.D. (eds), (1986). *Ecological Aspects of Social Evolution*, Princeton Univ. Press, Princeton, NJ.
- Sakura, O. (1991). On the concept of "group" in primates, with special reference to fission-fusion of chimpanzees. In: Ehara, A., Kimura, T., Takenaka, O., and Iwamoto, M. (eds.), *Primate Today*, Elsevier, Amsterdam, pp.247-250.
- Sakura, O. (in prep). On the concept of "group" of animals, with special reference to non-human primates: a proposal of the pluralistic terminology.
- Sakura, O. and Matsuzawa, T. (1991). Flexibility of nut-cracking behavior using stone hammers and anvils of wild chimpanzees: an experimental analysis. *Ethology* 87: 237-248.
- Sakura, O., Fushimi, T. and Sugiyama, Y. (1991). Party size of chimpanzees and food patch size: a preliminary study in Bossou, Guinea. Paper presented at the 7th meeting of Japan Primatology Society, Kawasaki Medical College, Kurashiki, Okayama.
- Sugiyama, Y. (1968). Social organization of chimpanzees in the Budongo

- forest, Uganda. *Primates* 9: 225-258.
- Sugiyama, Y. (1973). The social structure of wild chimpanzees: a review of field studies. In: Mitchel, R.P., and Crook, J.H. (eds.), *Comparative Ecology and Behavior of Primates*, Academic Press, London, pp.375-410.
- Sugiyama, Y. (1981). Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, 1979-1980. *Primates* 22: 435-444.
- Sugiyama, Y. (1984). Population dynamics of wild chimpanzees at Bossou, Guinea, between 1976-1983. *Primates* 25: 391-400.
- Sugiyama, Y. (1988). Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *Intl. J. Primatol.* 9: 393-407.
- Sugiyama, Y. (1989). Population dynamics of chimpanzees at Bossou, Guinea. In: Heltne, P.G. and Marquardt, L.G. (eds.), *Understanding Chimpanzees*, Harvard Univ. Press, Cambridge, MA, pp.134-145.
- Sugiyama, Y. and Koman, J. (1979). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20: 323-339.
- Sugiyama, Y. and Koman, J. (1987). A preliminary list of chimpanzees' alimentation at Bossou, Guinea. *Primates* 20: 513-524.
- Tutin, C.E.G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees. *Behav. Ecol. Sociobiol.* 6: 29-38.
- Tutin, C.E.G., McGrew, W.C. and Baldwin, P.J. (1983). Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates* 24: 154-173.
- Uehara, S. (1981). The social unit of wild chimpanzees: a reconsideration based on the diachronic data accumulated at Kasoje in the Mahale Mountains, Tanzania. *J. Afr. Studies* 20: 15-32.
- van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120-144.
- White, F. J. (1988). Party composition and dynamics in *Pan paniscus*. *Int.*

J. Primatol. 9: 179-193.

White, F.J. (1989). Ecological correlates of pygmy chimpanzee social structure. In: Standen, V. and Foley, R.A. (eds.), *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, Blackwell, Oxford, pp.151-164.

White, F.J. and Wrangham, R.W. (1988). Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* 105: 148-164.

Wrangham, R.W. (1975). The Behavioural Ecology of Chimpanzees in Gombe National Park. PhD thesis, Cambridge University.

Wrangham, R.W. (1977). Behaviour of feeding chimpanzees in the Gombe National Park, Tanzania. In: T.H. Clutton-Brock (ed.), *Primate Ecology*, Academic Press, London, pp. 503-538.

Wrangham, R.W. (1986). Ecology and social relationships in two species of chimpanzee. In: Rubenstein, D.I. and Wrangham, R.D. (eds.), *Ecological Aspects of Social Evolution*, Princeton Univ. Press, Princeton, NJ, pp.452-470.

Wrangham, R.W. and Smuts, B.B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fertil.*, Suppl. 28: 13-31.

Table 1. Age-sex structure of the chimpanzee community in Bossou.

Study period		Adults	Adolescents	Juveniles		Infants	Total
				late	early		
I (Sep. 1987	♂	1	1	3 - 2*	0	2	6 - 7
- Mar. 1988)	♀	8 (4)	0	0	2	3	13
	total	9	1	3 - 2*	2	5	19 - 20
II (Nov. 1989	♂	1	2	0	1	2	6
- Mar. 1990)	♀	8 (2)	0	2	1	3	14
	total	7	2	2	2	5	20

adult: 12_≤yrs old; adolescent: 8-11yrs old; early juveniles: 4-5yrs old;

late juveniles: 6-7yrs old; infants: 0-3yrs old.

* one juvenile male was died in December, 1987.

Table 2. Comparison of party size among *Ficus mucoso* and *Antiaris africana*.

Tree species	DBH(cm)	Canopy Diameter (m)	Chimp-minutes	Party size (mean)
<i>Ficus mucoso</i>	190	20	33.5	4.1
<i>Antiaris africana</i>	156	28	40	1.4

Table 3. The effect of the presence of estrous females on the distribution of males.

Period	Est _{♀♀}	N	% parties with ♂	% young♂ [*] independent	♂♂:♀♀ mean (SD)
I	yes	54	96.3	33.3	0.81 (0.585)
	no	94	61.7	7.5	0.45 (0.439)
			<i>P</i> <0.001	<i>P</i> <0.001	<i>P</i> <0.001
II	yes	124	92.7	39.5	0.60 (0.339)
	no	134	54.5	27.6	0.35 (0.480)
			<i>P</i> <0.001	<i>P</i> <0.05	<i>P</i> <0.001

* 'young males' represent adolescent and late juvenile males. See table 1 for detailed composition of age/sex class of the group.

FIGURE LEGENDS

Fig. 1. Relative frequency distribution of observed party sizes. Solid line: Period I, 1987-88 ($N=148$, one or two observers); Dotted line: Period II, 1989-90 ($N=258$, three or four observers).

Fig. 2. Monthly fluctuation of party sizes. Mean and *SD*. Solid line with circles: Period I; Dotted line with squares: Period II.

Fig. 3. The relation among party size and feeding ratio of a party. Relative frequency of party sizes of feeding party in a food patch in trees are shown. Hatched bars: parties of which feeding ratio was less than 50% ($N=37$); Open bars: more than equal 50% ($N=34$). Arrows represent medians.

Fig. 4. The effect of the presence of danger on the party size. Frequency distribution of sizes of party moving on ground are shown. Closed bars: in the situation of crossing roads (see text for details); Open bars: in forests; Arrows: medians.

Fig. 5. The effect of the presence of infants on affiliation among the chimps. Dendrogram was calculated by the ratio of sharing the same party of two females (see text for details) and with the Ward method cluster analysis. Rectangularized by single line: lactating female; Rectangularized by double line: cycling female; No rectangular: an adult male. Connection between *Ka* and *Ki* represents their mother-daughter relation.

Fig. 6. The ratio of a female foraged in the same party with the fully matured male, *TA*. Dotted bars: cycling females; Open bars: lactating. Left bars: Period I; Right: Period II.

Fig. 1

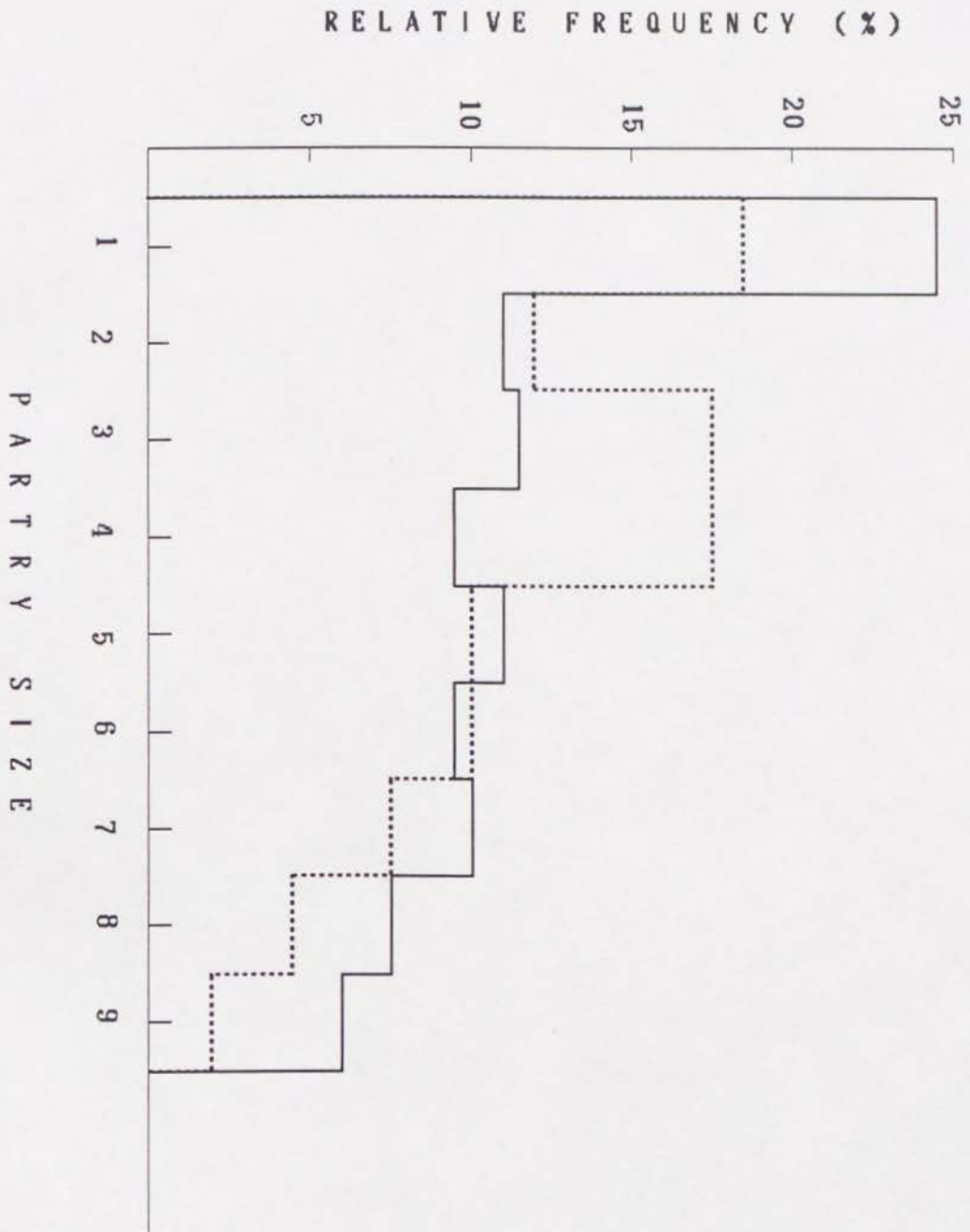


Fig. 2

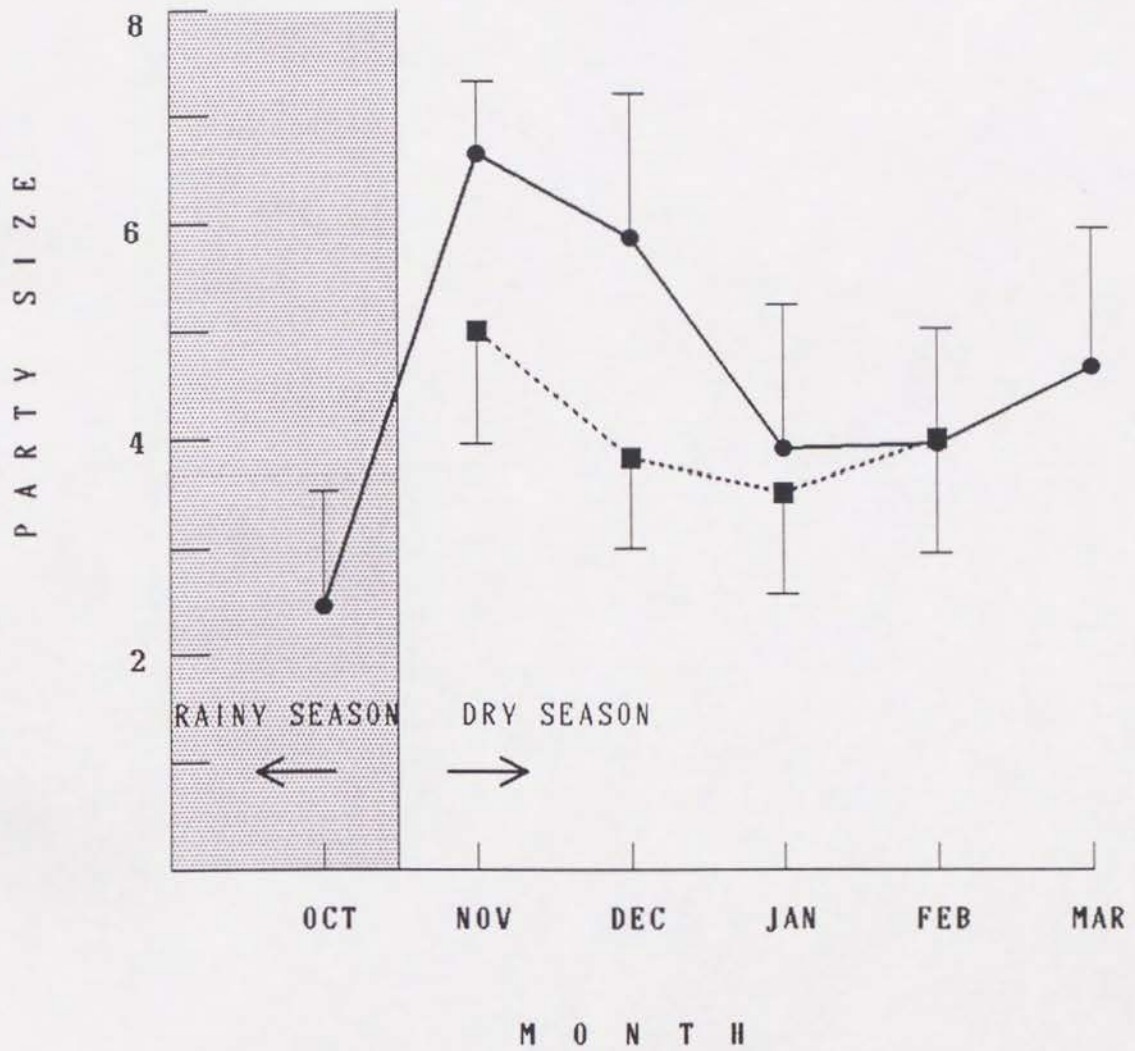


Fig. 3

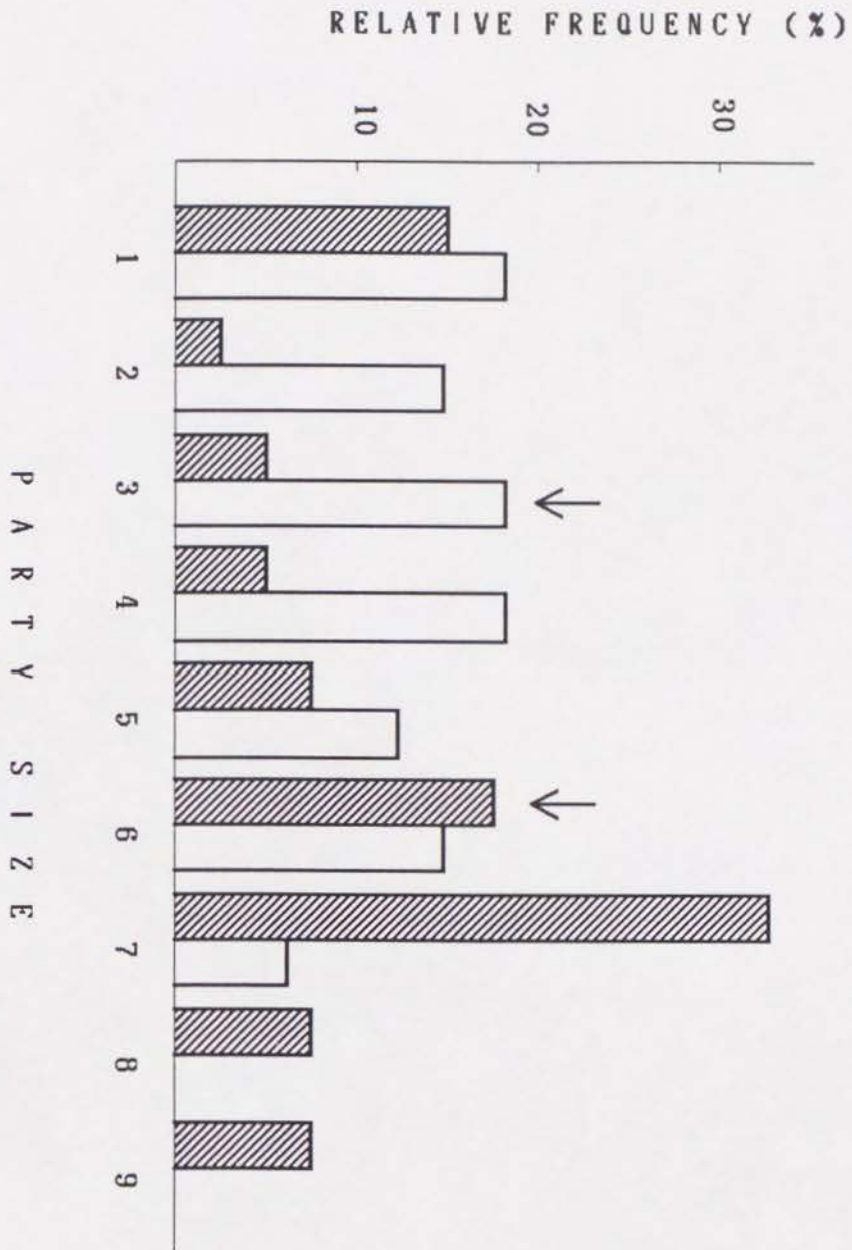


Fig. 4

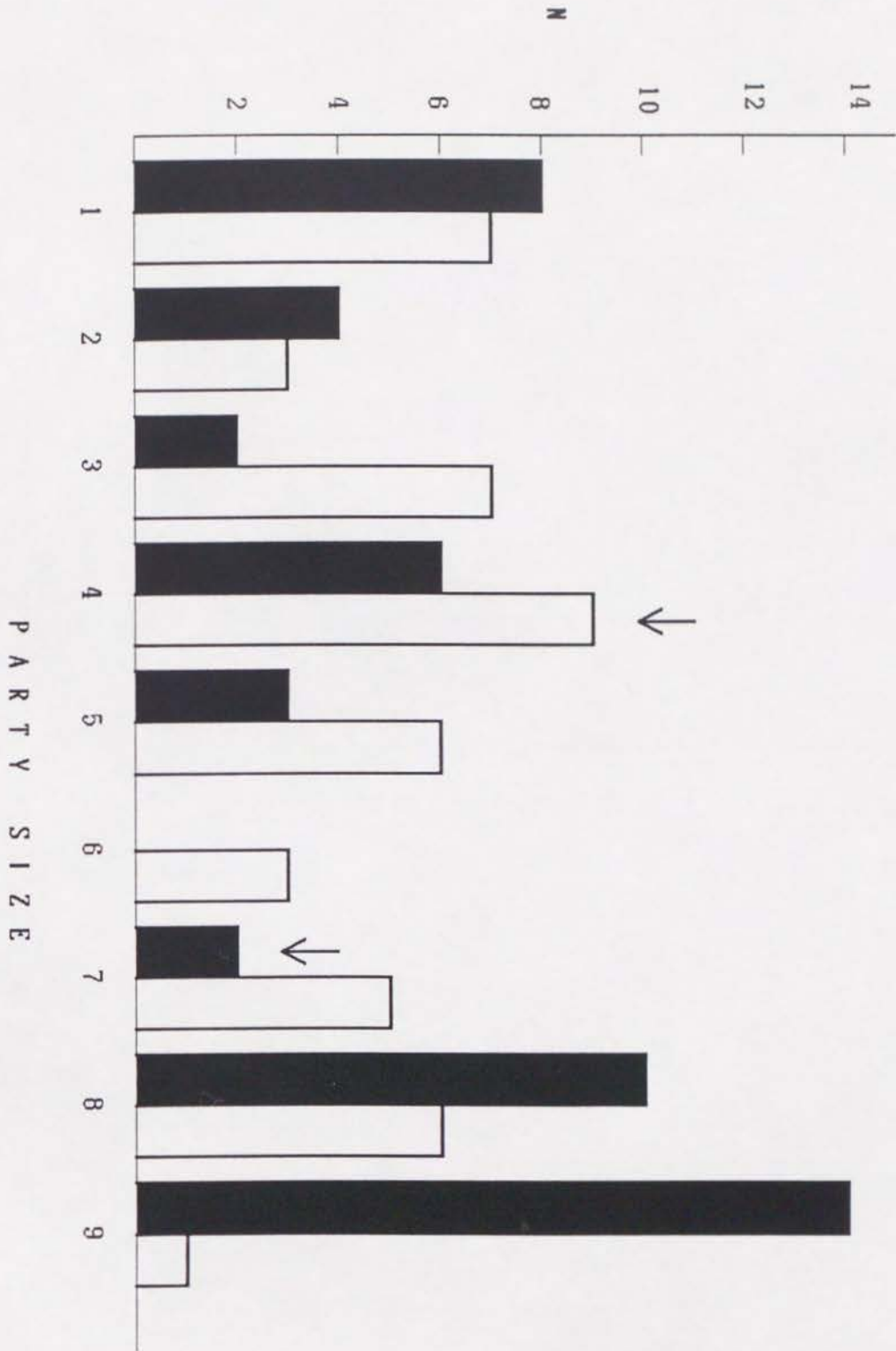
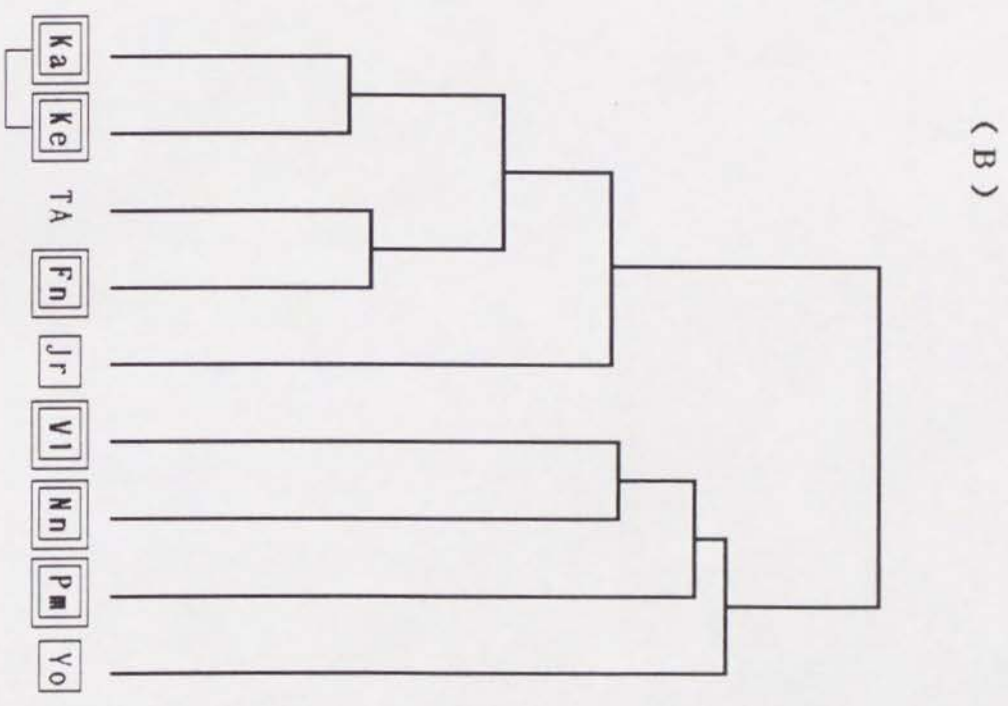
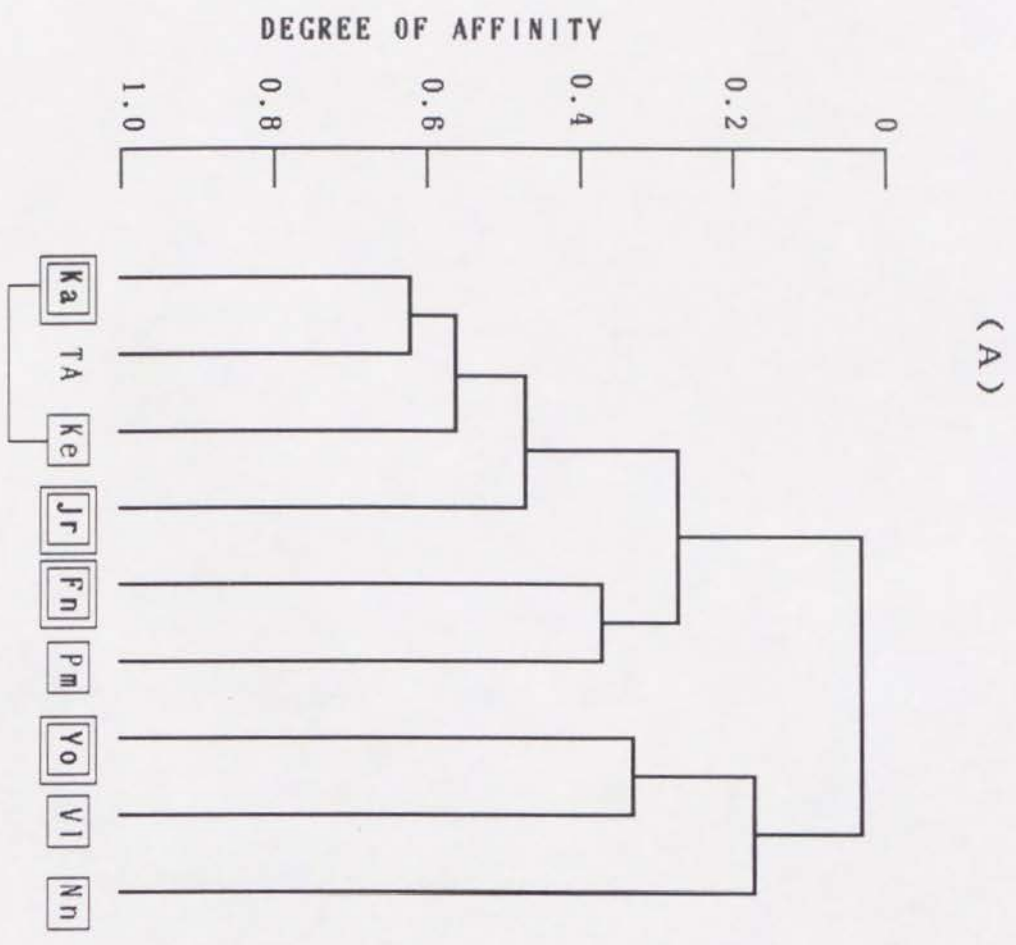


Fig. 5



% SHARING COMMON PARTIES WITH THE ALPHA MALE

