PRIMATES, 22(1): 70-83, January 1981

The Evolution and Socioecology of Dominance in Primate Groups: A Theoretical Formulation, Classification and Assessment

CLARA B. JONES
Marshall Foundation

ABSTRACT. Dominance hierarchies are presumed to evolve by individual selection from an evolutionary compromise between intraspecific competition for resources and for mates. The hypothesis is put forward that when competition in "stable" habitats leads to "niche breadth," a species is preadapted to life in heterogeneous environments and the consequent selection for fecundity. Status patterns are viewed as systems of signals communicating differential tendencies among individuals to attack or retreat, and a simple graphical model is presented which relates the costs or benefits to fitness of aggressive or appeasement behavior and interindividual distance. Primate societies are classified on the basis of their dominance hierarchies, and the ecological correlates of these patterns are discussed. Based on hypotheses presented in the paper, topics for future research are suggested.

INTRODUCTION

In the first discussion of dominance hierarchies in monkeys and apes, ZUCKERMAN (1932) noted the apparent relationship between sexual and status behavior. He argued that "the sexual responses of sub-human primates may have no connection with sexual appetite, and often appear to be used as a means to obtain material advantages, ... for example, food or protection from enemies.... The permanent bi-sexual associations of monkeys and apes form an adequate environment in which the complex sensori-motor equipments of these animals may evolve new types of social and sexual response. Sexual prostitution can be regarded as a means by which monkeys survive within a social framework that achieves a dynamic character by a system of dominance. In many cases the assumption of the female sexual attitude by one animal towards another implies that in this situation the 'presenting' animal is submissive to the other." ZUCKERMAN intuited three characteristics of dominance systems still recognized: (1) there is an evolutionary relationship between sexual behavior and status behavior; (2) these signals are often "ritualized"; and (3) there may be a competitive basis to the relations of males and females in groups. Most important, however, ZUCKERMAN suggested the notion that strategies of resource defense cannot be separated from strategies of reproduction.

WILSON (1975) points out that dominance hierarchies represent one outcome of contest competition. Competition occurs when two or more organisms actively demand a common, limited resource, usually food or mates. Different resource patterns lead to different effects.

Where resources are distributed evenly and predictably, selection will favor competitive ability (i.e., survivorship) and "social tolerance"; fecundity will be favored where resources are "unstable" in time and space (EMLEN, 1973; WILSON, 1975). Thus, mechanisms which may maximize reproductive rate (e.g., sexual selection1) and kin selection2)) will be most elaborate in heterogeneous habitats where populations are held at low levels and resource competition (selection for survivorship and crowding) is relaxed. These predictions have significant implications for the discussion of the socioecology of dominance which follows.

In the present paper, I will attempt to extend the argument that differences in the dominance strategies of individuals in primate groups ultimately represent an evolutionary compromise between intraspecific competition for resources and for mates. Following EMLEN (1973), I assume that status systems evolve by individual selection, that individuals assess their probabilities of winning and losing in competition with others in their sub-population, and that some lose less by settling for subordinance than they lose by continuing to compete. I have reviewed the functions of dominance systems elsewhere (JONES, 1980).

THE ECONOMICS OF DOMINANCE SIGNALS

A dominance hierarchy may be viewed as a system of signals communicating differential tendencies among individuals to attack or retreat. The system of status signals is employed by individuals to maximize survival and reproductive success. Thus, a signal will be expressed when the benefits (to fitness) of the behavior outweigh the costs (see BROWN, 1964). In some primate species, signal systems are subtly graded (MARLER, 1965), permitting individuals to communicate their intentions so economically that escalated aggression rarely occurs. Where species have not evolved signals permitting interindividual proximity without a high likelihood of aggression, social evolution may be restricted (OTTE, 1974).

Figure 1 expresses a simple graphical relationship for a hypothetical dyad between the costs or benefits to reproductive success of aggressive or appeasement signals and interindividual distance (see Fig. 2). Where individuals share a common space, for each interaction there will be a distance which maximizes fitness (benefits will be greater than costs). The shapes of the cost and benefit curves will determine the minimal distance permissible, and social species will have smaller mean minimal distances than non-social species. In short, individuals experience decreased fitness because they live together and demand common resources. Dominance hierarchies maximize the benefit to cost ratio of social dispersion where intraspecific competition within dyads occurs. What factors will determine the intensity of this competition and lead to the evolution of dominance hierarchies?

PREDATION, GROUP FORMATION AND SELECTION FOR DOMINANCE HIERARCHIES

Predation pressures may lead to the clumping of animals where they confront the problem of how to partition resources, though some species may form permanent groups where predation pressure is apparently low (e.g., squirrel monkeys, *Saimiri* spp.). Individuals may, thus, be clumped because habitats are seldom if ever uniform with respect to their resource distribution. Whether or not the distribution and abundance of food, in the absence of predation pressure, is sufficient to maintain groups once they have formed at clumped resources will be a function of the costs of assembling and disassembling a group for the utilization of resources compared to the costs of keeping a group intact. If the aggregation of in-

---

1) "Sexual selection" is the differential reproduction of genotypes which accrue large quantities of and/or high quality mates (see TRIVERS, 1972).

2) "Kin selection" is the differential survival and/or reproduction of genotypes of relatives other than offspring (see WEST-EBERHARD, 1975). I assume that nepotism will be favored where it replicates genotypes at a faster rate than selfish reproduction.

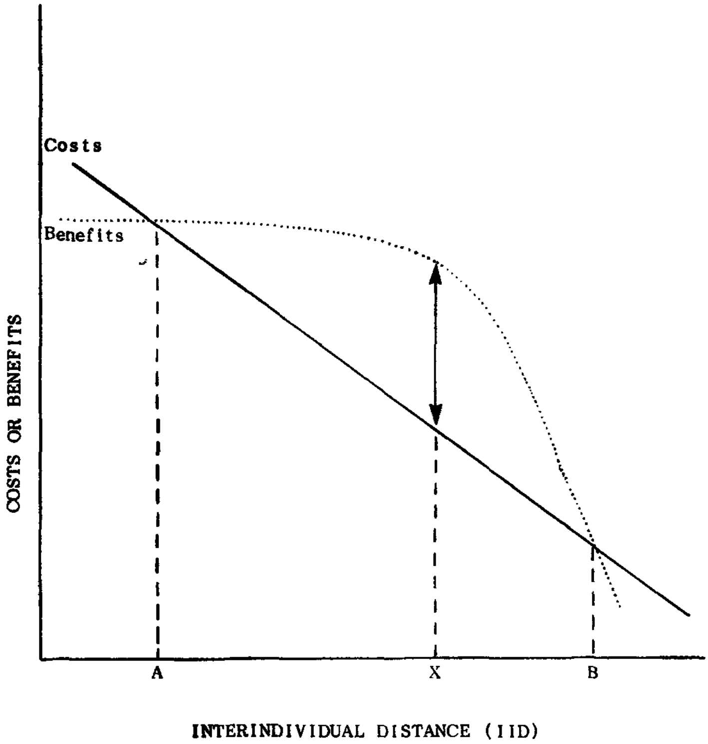

Fig. 1. This graphical model describes the costs or benefits to individual reproductive success of status behavior. As the distance between individuals decreases, the costs increase. The benefits will increase and then level off as the likelihood of escalated aggression increases with decreases in interindividual distance. For each interaction, the individual should coexist with others at distances between A and B (where benefits>costs) and the maximum net benefit (benefit-cost) will be at a distance of X. For any dyad, the shapes of the cost and benefit curves will vary with age, sex, degree of relatedness, individual experience, habitat, etc. (after DAVIES, 1978; JONES, 1978).

dividuals at clumped resources leads to the evolution of conventional signals to mediate interindividual aggression, costs might be minimized by individuals remaining assembled in groups of known composition where signalling approaches a predictable function of interindividual characteristics based on mutual recognition.

Dominance hierarchies are most likely to form where resources occur in patches that are not superabundant and not too widely separated in space and time (EMLEN, 1973). Under these circumstances, it will pay individuals to develop conventions permitting the most economical partitioning of resources given the relative abilities of individuals to defend an area within a patch for their exclusive use without the expensive expression of escalated aggression. Individuals able to assume the highest costs if escalated aggression should occur signal with highest intensity and are the most dominant. It will pay dominants and subordinates to obey the conventions of the hierarchical system of dominance signals since resources are not unlimited and time spent on aggression will be time not spent on feeding and mating ("aggressive neglect"). Escalated aggression would compound the expense of feeding and reproduction and increase the individual's energy requirements, a cost which the energy yield of a limited food supply may not be able to provide.

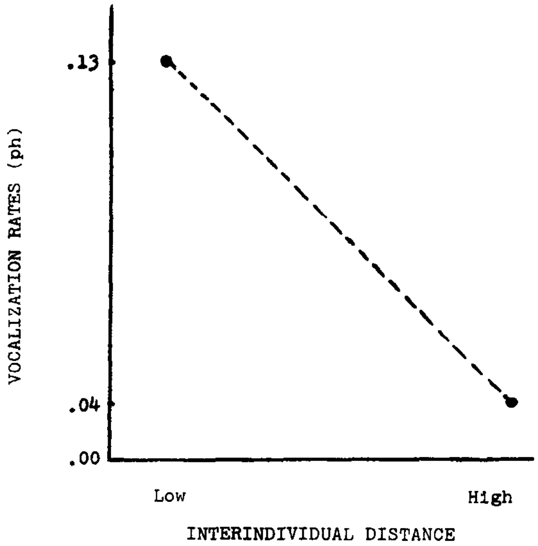

Fig. 2. Vocalization rates for a "beta" male when his interindividual distance from the "alpha" male is high and low. This graph roughly represents a cost curve as expressed in Figure 1 and is based on actual data (JONES, 1978).

SEXUAL SELECTION AND THE EVOLUTION OF DOMINANCE

Competition among males will be intense where females are clumped in space and time since male reproductive success will be limited only by the number of mates which each can control, while female reproductive success is limited by the amount of energy extractible from the environment that can be converted into offspring (OTTE, 1974). Where food and females are distributed unevenly, some males will control many more females than others.

OTTE (1974) makes the point that sexual selection modifies the communication system of any species and acts on males and females differently. Male status systems are usually more highly developed than female hierarchies because competition for resources is more intense in the former sex, males in a group are generally unrelated, and males can increase their reproductive output more than females can through social competition (EMLEN, 1973). Probably for these reasons, males are generally dominant to females in primates. Sexual selection, then, may determine the differential allocation of food resources to males and females, a condition that reinforces the theoretical point that the reproductive interests of the sexes are not identical (TRIVERS, 1972). This reproductive conflict between males and females is dependent upon the differential investment in offspring between the sexes and the greater variance in reproductive success among males.

Thus, male interests usually dominate female interests. Those males who are reproducing group members have "priority of access" to resources. It can be expected, however, that male selfishness will be limited by deleterious effects upon the reproductive success of females (DOWNHOWER & ARMITAGE, 1971) and that males may sometimes forego strategies optimal to their own sex in favor of those optimal for females (PARKER, 1974). These conditions may sometimes lead to rare forms of dominance systems. In these cases, intersexual selection (e.g., "female choice") may limit the number of males in primate units (PACKER & PUSEY, 1979; see RASMUSSEN, 1979) or, in a few instances, sexual selection may lead to the evolution of female dominance.

THE SOCIO-ECOLOGY OF DOMINANCE

Table 1 provides an ecological classification of primate displacement patterns where group dispersion is found. Despite recent advances in the ecological analysis of primate societies (see Clutton-Brock, 1977; Clutton-Brock & Harvey, 1977), their niches have not been quantified. Enough is known, however, to permit broad comparisons and contrasts on the basis of resource patterns and their defensibility. It is important to note that social structure may vary not only between species, but also between populations of the same species, presumably as a function of similarities and differences of ecological variables. For example, the common langur, *Presbytis entellus*, is found in one-male and multi-male organizations (Hrdy, 1977).

The first major group that can be differentiated includes only one mature, reproductive male. Five patterns of status system are evident. The first (I.A.) involves a male, a female and their young. The reproductive male controls his female and excludes other males from access to her. Females are usually aggressive, excluding other females and cooperating with the male in group defense (e.g., the siamang, *Symphalangus syndactylus*), though in some instances, individuals defend themselves by crypticity (e.g., the night monkey, *Aotus trivirgatus*). The male may invest significantly in his young, presumably as a strategy to maximize his reproductive success. Resources are predictable and evenly dispersed (e.g., *S. syndactylus*) (Chivers, 1977) or predictable and rare (e.g., the yellow-handed titi, *Callicebus torquatus*) (Kinzey, 1977), and if they are defensible (Brown, 1964), territoriality results (e.g., *C. torquatus*) (see Emlen & Oring, 1977).

Kinzey's (1977) recent discussion of the mainly frugivorous *C. torquatus* emphasizes the importance of rare food species, particularly *Brosimum*, *Jessenia polycarpa* and *Pithecolobium*.

Table 1. A socioecological classification of primate dominance patterns. Refer to text for explanation and references.

- I. One mature male
  - A. Group male controls access to one adult female and excludes all other adult males. Resources limited, dispersed and predictable or rare and defensibly clumped.
  - B. Group male controls access to more than one adult female and excludes all other males. Food resources distributed in patches, sparse abundance.
    - 1. Males dominant to females, age correlates negatively with rank for females.
    - 2. Age correlates positively with rank for females.
      - a. Females dominant to males.
      - b. Males dominant to females.
  - C. Group male controls access, from other mature males, to more than one adult female and tolerates presence of younger, subordinate males who may be his kin and who may or may not share access to females. Males cooperate in group defense. Resources distributed in patchy manner, variable abundance and predictability in space and time.
- II. More than one adult males coexist with multiple females on range or territory. Most terrestrial. Resources either patchy with local abundances, clumped in variable patch sizes but widely dispersed or unpredictable in space and time.
  - A. Adult males of group arranged in dominance hierarchy and cooperate in group defense. Adult males compete for copulations.
    - 1. Males dominant to females, age correlates negatively with rank and a single linear hierarchy.
    - 2. Females dominant to males, age correlates positively with rank and a single linear hierarchy.
    - 3. Males dominant to females and age correlates positively with rank.
      - a. Males and females rarely interact. Intersexual dominance hierarchies separate.
      - b. Males and females interact within single linear hierarchy.
  - B. Males may or may not coexist with females, seldom compete for copulations and do not control mates. Males dominant to females; age correlates positively with rank.

In contrast, the non-territorial *S. syndactylus* utilizes a more even supply of food, ingesting more leaves and a greater variety of items than the territorial titi (Chivers, 1977). However, food resources in both species are apparently distributed such that males cannot increase their fitness by investing energy to control more mates (see Emlen & Oring, 1977), and, following the argument expressed above, the stability of resources at this level of organization favors selection for survivorship and "social tolerance" over fecundity.

The second major subset of species (I.B.) includes one mature male and more than one adult female. Again, a single male excludes all other adult males from the group and from access to females. Males and females may share group defense (e.g., the lepilemur, *Lepilemur mustelinus*) or defense may be unisexual as for the common langur (*Presbytis entellus*), where group defense is a female trait (Hrdy & Hrdy, 1976). Alternatively, animals may defend themselves by escape (e.g., the patas, *Erythrocebus patas*) or predation pressure may be low (e.g., the black and white colobus, *Colobus guereza*). Food resources are distributed in a patchy manner with sparse abundance (see Emlen & Oring, 1977; Wilson, 1975). The one-male organization is said to be an adaptation to "stressful" conditions in primates (Jolly, 1972). Many species with this structure are primarily folivores with a narrow niche or live in xeric habitats, extreme conditions that should favor polygyny and the elaboration of sexual selection to maximize fecundity (Emlen, 1973).

For most of the species of type I.B., males are dominant to females and age correlates positively with rank (e.g., the hamadryas baboon, *Papio hamadryas*) (Kummer, 1968; I.B.2.b., Table 1). For *Presbytis entellus* females, however, age correlates negatively with rank (I.B.1., Table 1). Hrdy and Hrdy (1976) suggest that this age-reversed status system evolved by kin selection and represents a case in which dominance correlates with reproductive value (see Wilson, 1975). Apparently, older females maximize their inclusive fitness by "altruistically" deferring to younger relatives.

Where individuals are closely related, it may benefit elders to restrain selfish behavior because of the high likelihood of behaving selfishly toward kin (see West-Eberhard, 1975). It is expected that females will be more "altruistic" than males since competition among them is normally less intense and since, unlike males, they can discriminate their own offspring in polygynous societies. By way of the dominance hierarchy, then, kin selection may influence the differential allocation of energy and nutrients to relatives in accordance with their reproductive potential (West-Eberhard, 1975). The reversed-age status pattern may be rare because females in most societies are not related closely. Certainly this is the case for *P. hamadryas* where young females are "adopted" from several different groups by a male for his future harem (Kummer, 1968).

For the patas monkey (*E. patas*) (Hall, 1968; I.B.2.a., Table 1), females are dominant to males, a unique pattern among one-male groups. The patas inhabits seasonal and arid habitats. These primarily herbivorous primates have apparently adopted female dominance as a strategy to maximize the fecundity of females and, thereby, males' reproductive success.

The evolution of three distinct dominance patterns for the one-male social unit (Table 1) suggests that mechanisms have different costs and benefits (to fitness) in different ecological regimes. In all cases, selection for polygyny is apparently intense, but consequences vary. For example, while the range of group size and sexual composition is about identical for hamadryas and patas (about 1♂/3♀♀ to about 1♂/13♀♀), males of the latter species may have been forced to adopt subordinance in order to achieve such ratios. Larger ratios are apparently achieved in *P. entellus* through the association of female relatives in age-reversed hierarchies and use by males of infanticide against unrelated offspring (SUGIYAMA, 1967; HRDY, 1977; CHAPMAN & HAUSFATER, 1979; HAUSFATER, SAUNDERS & CHAPMAN, in press). It will be hypothesized below that adaptation to variable habitats such as those inhabited by some one-male primate units may have been achieved by the preadaptation of ancestors living in "stable," wet forest conditions with "broad" ecological niches (i.e., "phenotypic plasticity"; EMLEN, 1973).

Recently, the one-male group in mammals has assumed importance as a model for the genetical evolution of social behavior (MCCRACKEN & BRADBURY, 1977; SCHWARTZ & ARMITAGE, 1980). While within-group genetic variance may be low in these societies, genetic heterogeneity between generations and groups is apparently high (but see FROEHLICH & THORINGTON, in press). Thus, the fixation of characters (by genetic drift, founder effects or other mechanisms; e.g., kin selection) may be prevented at the population level. These reports suggest that the major factors maintaining heterogeneity between sub-units of a population may be the rates of individual exchange between groups, particularly patterns of juvenile dispersal, the length of male tenure (see CHAPMAN & HAUSFATER, 1979), and the avoidance of inbreeding. Electrophoretic analyses of primate societies are needed to determine the relevance of this model for the order.

The status system type I.C. is sometimes termed the "age-graded" pattern (EISENBERG, MUCKENHIRN & RUDRAN, 1972). This system involves one mature male who controls access to more than one adult female to whom he is dominant. One or more immature males, subordinate to the group leader, coexist in the group and share in group defense. Kin selection may contribute to the evolution of this status pattern since immature males are presumed to be group offspring and may share females sexually with the dominant male. Where this pattern of displacement exists, resources are distributed in a patchy manner with variable abundance and predictability in time and space (see GOODALL, 1977). The age-graded status system may be intermediate in evolution between one-male groups where all juvenile offspring are dispersed and multi-male status systems (type II., Table 1) in which juvenile dispersal is accompanied by the cooperation of presumably unrelated adult males.

A. GOODALL's recent report (1977) of the feeding ecology of the gorilla (*Gorilla gorilla beringei*) suggests that status system I.C. may have evolved in response to "preferred" plant food which he shows to be "rare" and patchily distributed. Major food items show a "wide and plentiful distribution" but are seasonally available. Thus, food may not be sufficiently predictable or abundant in time and space to support a larger, more complex social organization than the "graded" one-male system. Further, environmental heterogeneity (e.g., seasonal availability of food) may be expected to hold gorilla populations at low levels so that selection for competitive ability and crowding is less significant than selection for reproductive rate. The age-graded system, thus, apparently evolves to maximize fecundity and the potential for polygyny. Kin selection and sexual selection may function in concert to produce this displacement pattern.

Species of type II (Table 1) consist of more than one adult male coexisting with multiple females on a home range or territory (Fig. 3). Males usually do, and females may or may not, move between groups (A. JOLLY, pers. comm.). Most of these species are terrestrial, living in areas where predation pressure is presumably high (see CLUTTON-BROCK & HARVEY, 1977). Resources may be patchy with local abundances, clumped in variably-sized patches but widely dispersed, or unpredictable in space and time (EMLEN & ORING, 1977).

Older individuals are usually dominant to younger adults (WILSON, 1975). In the mantled

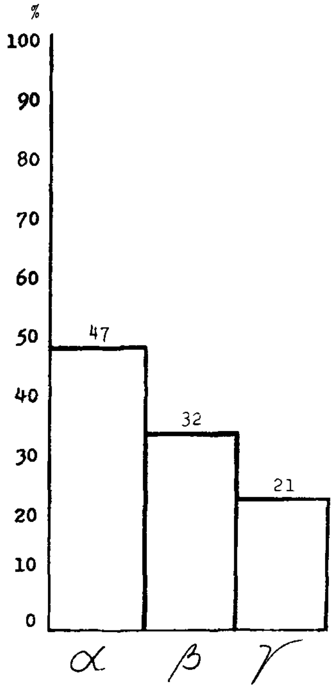

Fig. 3. In multi-male groups, male rank may or may not correlate with copulation success (Kolata, 1976). In the mantled howler monkey, it does. This figure shows the proportions of total copulations ($N = 34$) achieved by the "alpha," "beta" and "gamma" males of a three-male group inhabiting riparian habitat in Neotropical dry forest (Jones, 1978).

howler monkey (*Alouatta palliata* Gray), however, a rare form of social organization is found in which age correlates negatively with rank for both sexes (type II, A.1., Table 1; Jones, 1980). Like the dominance hierarchies in most primate groups, males are dominant to females and a single linear system is evident.

Howler monkeys, wholly herbivorous primates, are generally classified as "arboreal folivores," though they prefer to eat a diet of leaf flush, flowers and fruit. Apparently, this niche breadth, in addition to the ephemeral nature of preferred resources, have favored a complex group structure unlike the one-male system typical of folivorous primates who utilize a more monotonous and evenly-dispersed diet.

Howler monkeys are apparently food limited by the availability of palatable leaves and by allelochemicals (Glander, 1975), and intense intraspecific competition for these resources may have created a condition in which the costs of aggressive behavior to fitness are high, and the survival benefits of high rank to younger individuals are greater than those to elders (Jones, 1980). Young adult howler monkeys, thus, may compete more intensely for dominance. That age-reversed status systems are rare may indicate that fitness is generally maximized in association with large body size and strength. Sometimes, however, life history strategy may favor early adult stages over later ones (see Hausfater, Saunders & Chapman, in press). The specific environmental determinants of such age-reversed patterns have not been demonstrated, though the distribution and abundance of palatable, mature leaves are implicated since this dominance pattern has been identified so far only in folivores. A further similarity between common langurs and mantled howlers suggests that the age-reversed system may be related to the genetic and physiological stresses occasioned by extreme phenotypic plasticity, apparently permitting adaptation to a broad range of habitats.

Thus, as mentioned above, one possible outcome of selection for survival in stable habitats, niche breadth (i.e., "behavioral plasticity"), may allow mantled howler monkeys, as well as other species, to cope with environmental unpredictability in unstable areas. Since it may be assumed that, where they expand their range, species will radiate from more to less stable conditions (WILSON, 1975), those characterized by phenotypic heterogeneity in predictable habitats will be preadapted to other conditions. Howler monkeys, for example, may be found in one-male (CHIVERS, 1969), age-graded (EISENBERG, MUCKENHIRN & RUDRAN, 1972), as well as multi-male (CARPENTER, 1934) organizations, apparently as a result of ecological factors (WILSON, 1975), and the species ranges from Neotropical rain forest to tropical dry deciduous habitat.

A rare type of status system is outlined in II.A.2 (Table 1). Occasionally, females are dominant to males. This system has been identified in seven primate species with multi-male organization: the indri (*Indri indri*) (POLLOCK, 1979); the pygmy marmoset (*Cebuella pygmaea*) (CHRISTEN, 1974); the ring-tailed lemur (*Lemur catta*) (JOLLY, 1966)[3]; Verreaux's sifaka (*Propithecus verreauxi*) (RICHARD, 1973); the talapoin (*Cercopithecus talapoin*) (WOLFHEIM, 1975); the vervet (*Cercopithecus aethiops*) and the blue monkey (*C. mitis*) (ROWELL, 1971). Similarities between the last two species suggest that selection for survivorship and "niche breadth" in "stable" habitats may have resulted in the evolution of this status pattern and preadaptation to "unstable" conditions. *C. aethiops* and *C. mitis* are the only members of the genus distributed in its extreme northern and southern ranges (GARTLAN & BRAIN, 1968). Since these species are found throughout the range of *Cercopithecus* monkeys as well as at the extremes, competition for resources may have displaced them from preferred rainfall forest into suboptimal areas of unpredictable habitat, semi-savannah forests with patchy distributions of food resources. Males may have adopted subordinance to females as a strategy to maximize survival in stable forests, a trait that would enhance female fecundity and their own reproductive success in variable habitats. That female dominance is so rare suggests that male deference to females benefits male reproductive success only occasionally and that the benefits from other strategies to maximize fitness are greater. The ecology and behavior of several species with female dominance are discussed in CLUTTON-BROCK (1977). These reports strongly reinforce the proposed hypothesis (that adaptation through "niche breadth" in predictable habitats led to preadaptation to unpredictable habitats) since the indri, the ring-tailed lemur and Verreaux's sifaka are all shown to occupy broad niches.

In species of type II.A.3. (Table 1), males are dominant to females and age correlates positively with rank for both sexes. In some cases (type II.A.3.a., Table 1: e.g., the Japanese macaque, *Macaca fuscata*), the sexes rarely interact (PACKER & PUSEY, 1979). Apparently, intersexual competition for resources has sometimes resulted in the displacement of males from females in space. The advantages of displacement, however, are not great enough to prevent intersexual group formation, and relations between the sexes are characterized by mutual avoidance and, presumably, resource partitioning. In these species, males defend females and offspring. This displacement strategy may be intermediate in evolution between that described in type II.A.3.b. (Table 1) and an extreme form of II.A.3.a. exemplified by the spider monkey (*Ateles geoffroyi*) in which spatial and temporal sexual segregation occurs

---

[3] A. JOLLY suggests (pers. comm.) that female dominance is a phylogenetic trait among the lemurs.

during foraging, and females "mimic"[4] males in size and genitalia, apparently as a form of predator defense (see GEIST, 1972).

KAWAI's (1958) discussion of dominance relations in *M. fuscata* suggests that kin selection may be responsible for the "nepotistic" pattern (see HAUSFATER, SAUNDERS & CHAPMAN, in press) in which younger female offspring assume positions in the hierarchy just below their mother and in inverse order of their birth (i.e., younger sisters are dominant to older sisters). Thus, the inclusive fitness of older sisters is apparently favored by kin selection to increase the fitness of younger sisters.

Apparently in the majority of species of type II.A.3., males and females interact within a single linear hierarchy (e.g., the rhesus macaque, *Macaca mulatta*) (II.A.3.b., Table 1). Resources may be sufficient to minimize competition between the sexes so that they coexist without spatial displacement. LINDBURG (1977) reports a catholic herbivorous diet for *M. mulatta* and preferred food is distributed in large, dispersed packages or in variably abundant, continuous vegetation. A broad niche may be a necessary condition in the evolution of complex sociality such as that characterizing multi-male primate groups (HAMILTON, BUSKIRK & BUSKIRK, 1978) and may provide a social "buffer" against environmental heterogeneity in the manner hypothesized above. Like Japanese macaques, *M. mulatta* has a nepotistic dominance system which has been described in detail by SADE (1972). In rhesus macaques, however, unlike *M. fuscata*, male rank does not appear to be strongly determined by maternal rank. SADE (1972) observed that the dominance system in *M. mulatta* maintains its order over time whether or not the mother is present, apparently demonstrating that the nepotistic pattern benefits sisters as well as mothers. The universal success of the *Macaca* genus and the generalized diets characterizing its species reinforces the major hypothesis of this paper and suggests that field studies of rain forest species should be carried out to determine the preconditions for phenotypic plasticity.

Perhaps the rarest system of all is detailed in II.B. In this pattern of displacement, males may or may not coexist with mates, and, though they are dominant to females, do not control them. Chimpanzees (*Pan troglodytes*) may be the only example of this system. The complex social behavior exhibited by this species is apparently related to the utilization of an extremely broad range of food types and distributional patterns, from insects requiring a solitary foraging technique, to superabundant, widely-spaced and ephemeral packages of flowers and fruit, to "hunting" (WRANGHAM, 1977; KAWABE, 1966; SUZUKI, 1966).

J. GOODALL (1965) found that status interactions were unusual among the individuals she studied, particularly among females. That this is so may reflect the observation that females and males are often found in kin associations[5], a pattern of displacement which would not favor the expression of aggression (WEST-EBERHARD, 1975). Further, dominance interactions would only be evident on limited and not superabundant resources. Dominance hierarchies may not be obvious at most times in the chimpanzee because the favored resources of this species appear to be superabundant packages of fruit with "irregular" phenological patterns,

---

[4] I. S. BERNSTEIN (pers. comm.) points out that communication may involve the issue of "cheating." This important topic is discussed by OTTE (1974) and DAWKINS and KREBS (1978).

[5] SCHOENER (1971) makes the point that kin selection may produce group sizes sub-optimal for foraging, a condition which may maintain chimpanzees and other species at relatively low levels of population density.

leading to selection for cooperative food-finding and utilization and against aggressive behavior.

One feature of chimpanzee social behavior which has been noted repeatedly is their apparent sexual promiscuity and the lack of intermale conflict over potential mates (WILSON, 1975). TUTIN (1980) discusses this and other strategies of reproduction in *Pan* and shows how mate choice and social dispersion may decrease intraspecific competition for food and mates. Sexual dimorphism in the chimpanzee is remarkably low, and this trait may be the effect of females foraging alone and "mimicing" male size for defense or of selection on "preferred," superabundant resources depressing the effects of sexual selection. Nonetheless, it appears that in the chimpanzee, as in other species discussed above, niche breadth as a strategy to maximize fitness in stable, tropical rain forest habitats preadapted *Pan* to survival in heterogeneous forests. Kin selection and resource distribution apparently interacted to produce a remarkably non-aggressive animal.

CONCLUSIONS

In summary, dominance hierarchies evolve where individuals compete in groups over clumped, limited resources. Through assortative distribution of resources on the basis of rank, individuals maximize their chances for survival and reproductive success by assessing their chances to win or lose in competition with other group members. Intraspecific competition for food may depress the effects of sexual selection if resources are predictably distributed or if resource dispersion favors sexual segregation during foraging and female defense without male protection. Where intraspecific competition for resources is not intense and populations are held at low levels by environmental unpredictability, selection for fecundity will be favored.

This paper has reviewed the forms that status hierarchies take in primate groups and provides a theoretical framework for the functional analysis of these signal systems. Table 1 suggests that a continuum may exist from less to greater patchiness in the distribution of resources, less to greater variability in the abundance of resources, smaller to greater "niche breadth" ("phenotypic plasticity"), and less to greater omnivority. These factors are apparently correlated with the size and social complexity of primate groups. When the resource parameters of given populations are quantified, as they have been for some birds (CODY, 1974), a more formal analysis of the social ecology of status patterns in primates can be made (see WILEY & WASER, 1980; HAUSFATER, SAUNDERS & CHAPMAN, in press).

The present paper suggests several areas for future research since the variables discussed are, on whole, deduced from current theory (WILSON, 1975) and remain untested for primates. Among the topics suggested are the degree and nature of spatial and temporal displacement and overlap of males and females, the degree and form of resource partitioning among sympatric species, the signal systems used to communicate information during status interactions and how these contribute to differential reproductive success (quantified in calories or offspring).

Acknowledgements. I thank IRWIN BERNSTEIN, GLENN HAUSFATER and ALISON JOLLY for extensive comments on an early draft of this manuscript. The work was made possible by a grant from the Marshall Foundation.

REFERENCES

Brown, J. L., 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.*, 76: 160–169.

Carpenter, C. R., 1934. A field study of the behavior and social relations of howling monkeys. *Comp. Psychol. Monog.*, 10: 1–168.

Chapman, M. & G. Hausfater, 1979. The reproductive consequences of infanticide in langurs: a mathematical model. *Behav. Ecol. & Sociobiol.*, 5: 227–240.

Chivers, D., 1969. On the daily behavior and spacing of free-ranging howler monkey groups. *Folia. Primatol.*, 10: 48–102.

———, 1977. The feeding behaviour of siamang (*Symphalangus syndactylus*). In: *Primate Ecology*, T. H. Clutton-Brock (ed.), Academic Press, New York, pp. 355–383.

Christen, A., 1974. Reproductive biology and behavior of *Cebuella pygmaea* and *Tamarin tamarin*. Fortscrift Verhaltensforsch. *Beihefte Z. Tierpsychol.*, 14: 1–80.

Clutton-Brock, T. H. (ed.), 1977. *Primate Ecology*. Academic Press, New York.

——— & P. H. Harvey, 1977. Primate ecology and social organization. *J. Zool.*, London, 183: 1–39.

Cody, M. L., 1974. *Competition and the Structure of Bird Communities*. Princeton Univ. Press, Princeton, New Jersey.

Davies, N. B., 1978. Ecological questions about territorial behaviour. In: *Behavioural Ecology*, J. R. Krebs & N. B. Davies (eds.), Sinauer Associates, Sunderland, Massachusetts, pp. 317–350.

Dawkins, R. & J. Krebs, 1978. Animal signals: information or manipulation. In: *Behavioural Ecology*, J. R. Krebs & N. B. Davies (eds.), Sinauer Associates, Sunderland, Massachusetts, pp. 282–312.

Downhower, J. & K. Armitage, 1971. The yellow-bellied marmot and the evolution of polygamy. *Amer. Naturalist*, 105: 355–370.

Eisenberg, J. H., N. A. Muckenhirn & R. Rudran, 1972. The relation between ecology and social structure in primates. *Science*, 176: 863–874.

Emlen, J. M., 1973. *Ecology: An Evolutionary Approach*. Addison-Wesley Pub. Co., Reading, Massachusetts.

Emlen, S. T. & L. Oring, 1977. Ecology, sexual selection and the evolution of mating systems. *Science*. 197: 215–223.

Froehlich, J. W. & R. W. Thorington, Jr., in press. The genetic structure and socio-ecology of howler monkeys (*Alouatta palliata*) on Barro Colorado Island. In: *Ecology of Barro Colorado Island: Seasonal Rhythms and Long-term Changes in a Tropical Forest*, E. G. Leigh, Jr. & A. S. Rand (eds.), Smithsonian Institution Press, Washington, D.C.

Gartlan, J. & C. Brain, 1968. Ecology and social variability in *Cercopithecus aethiops* and *Cercopithecus mitis*. In: *Primates: Studies in Adaptation and Variability*, P. Jay (ed.), Holt, Rhinehart & Winston, New York, pp. 253–292.

Geist, V., 1972. A comparison of social adaptations in relation to ecology in gallinaceous bird and ungulate societies. *Ann. Rev. Ecol. Syst.*, 8: 193–207.

Glander, K., 1975. Habitat and resource utilization: an ecological view of social organization in mantled howling monkeys. Ph.D. Dissertation, Univ. of Chicago, Illinois.

Goodall, A., 1977. Feeding and ranging behaviour of a mountain gorilla group (*Gorilla gorilla beringei*) in the Tsibinda-Kahuzi Region (Zaire). In: *Primate Ecology*, T. Clutton-Brock (ed.), Academic Press, New York, pp. 450–480.

Goodall, J., 1965. Chimpanzees of the Gombe Stream Reserve. In: *Primate Behavior*, I. DeVore (ed.), Holt, Rhinehart & Winston, New York, pp. 425–473.

Hall, K. R. L., 1968. Behaviour and ecology of the wild patas monkey, *Erythrocebus patas*, in Uganda. In: *Primates: Studies in Adaptation and Variability*, P. Jay (ed.), Holt, Rhinehart & Winston, New York, pp. 32–119.

Hamilton, W. J., R. E. Buskirk & W. H. Buskirk, 1978. Omnivory and utilization of food resources by Chacma baboons, *Papio ursinus*. *Amer. Naturalist*, 112: 911–924.

Hausfater, G., C. D. Saunders & M. Chapman, in press. Computer models of primate life-histories. In: *Natural Selection and Social Behavior*, R. D. Alexander & D. Tinkle (eds.), Univ. of Michigan Press, Ann Arbor.

HRDY, S. B., 1977. Infanticide as a primate reproductive strategy. *Amer. Sci.*, 65: 40–49.

——— & D. B. HRDY, 1976. Hierarchical relations among female Hanuman langurs (Primates: Colobinae, *Presbytis entellus*). *Science*, 1973: 913–915.

JOLLY, A., 1966. *Lemur Behavior*. Chicago Univ. Press, Illinois.

———, 1972. *The Evolution of Primate Behavior*. Macmillan, New York.

JONES, C. B., 1978. Aspects of reproductive behavior in the mantled howler monkey (*Alouatta palliata* GRAY). Ph.D. Dissertation, Cornell Univ., Ithaca, New York.

———. 1980. The functions of status in the mantled howler monkey, *Alouatta palliata* GRAY: Intraspecific competition for group membership in a folivorous Neotropical primate. *Primates*, 21: 389–405.

KAWABE, M., 1966. One observed case of hunting behavior among wild chimpanzees living in the savanna woodland of Western Tanzania. *Primates*, 7: 393–396.

KAWAI, M., 1958. On the system of social ranks in a natural troop of Japanese monkeys (I, II). *Primates*, 1: 111–148.

KINZEY, W. G., 1977. Diet and feeding behaviour of *Callicebus torquatus*. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, New York, pp. 127–152.

KOLATA, G. B., 1976. Primate behavior: sex and the dominant male. *Science*, 191: 55–56.

KUMMER, H., 1968. *Social Organization of Hamadryas Baboons. A Field Study. Biblioteca Primatologica*, Vol. 6, S. Karger, Basel.

LINDBURG, D. G., 1977. Feeding behaviour and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in North India. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, New York, pp. 223–250.

MARLER, P., 1965. Communication in monkeys and apes. In: *Primate Behavior*, I. DEVORE (ed.), Holt, Rhinehart & Winston, New York, pp. 544–584.

MCCRACKEN, G. & J. BRADBURY, 1977. Paternity and genetic heterogeneity in the polygamous bat, *Phyllostomus hastatus*. *Science*, 198: 303–306.

OTTE, D., 1974. Effects and functions in the evolution of signaling systems. *Ann. Rev. Ecol. Syst.*, 385–417.

PACKER, C. & A. E. PUSEY, 1979. Female aggression and male membership in troops of Japanese macaques and olive baboons. *Folia Primatol.*, 31: 212–218.

PARKER, G., 1974. Courtship persistence and female-guarding as male time-investment strategies. *Behaviour*, 48: 157–184.

POLLOCK, J. I., 1979. Female dominance in *Indri indri*. *Folia Primatol.*, 31: 143–164.

RASMUSSEN, D. R., 1979. Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). *Anim. Behav.*, 27: 1098–1112.

RICHARD, A., 1973. The social organization and ecology of *Propithecus verreauxi*. Ph.D. Dissertation, Univ. of London.

ROWELL, T. E., 1971. Organization of caged groups of *Cercopithecus* monkeys. *Anim. Behav.*, 19: 625–645.

SADE, D. S., 1972. A longitudinal study of social behavior of rhesus monkeys. In: *The Functional and Evolutionary Biology of Primates*, R. TUTTLE (ed.), Aldine, New York, pp. 378–398.

SCHOENER, T. W., 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.*, 2: 369–404.

SCHWARTZ, O. A. & K.B. ARMITAGE, 1980. Genetic variation in social mammals: the marmot model. *Science*, 207: 665–667.

SUGIYAMA, Y., 1967. Social organization of Hanuman langurs. In: *Social Communication Among Primates*, S. A. ALTMANN (ed.), Univ. of Chicago Press, Illinois, pp. 221–236.

SUZUKI, A., 1966. On the insect-eating habits among wild chimpanzees living in the savanna woodland of Western Tanzania. *Primates*, 7: 481–487.

TRIVERS, R., 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man*, B. CAMPBELL (ed.), Aldine, Chicago, pp. 136–179.

TUTIN, E. G., 1980. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.*, 6: 29–38.

WEST-EBERHARD, M. J., 1975. The evolution of social behavior by kin selection. *Quart. Rev. Biol.*, 50: 1–33.

WILEY, R. H. & P. WASER, 1980. Mechanisms and evolution of spacing in animals. In: *Handbook of*

Behavioral Neurobiology, Vol. 3, P. MARLER & J. G. VANDENBERGH (eds.), Plenum, New York, pp. 159–223.

WILSON, E. O., 1975. *Sociobiology: The New Synthesis.* Harvard, Cambridge.

WOLFHEIM, J. G., 1975. Activity patterns and sex differences in behavior of talapoin monkeys (*Miopithecus talapoin*). Ph.D. Dissertation, Univ. of California, Berkeley.

WRANGHAM, R. W., 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: *Primate Ecology*, T. CLUTTON-BROCK, Academic Press, New York, pp. 504–538.

ZUCKERMAN, S., 1932. *The Social Life of Monkeys and Apes.* Harcourt, Brace, New York.

—Received *April 16, 1980*; Accepted *July 31, 1980*

Author's Name and Address: CLARA B. JONES, *Marshall Foundation, 1406 East Front Street, Plainfield, New Jersey 07062, U.S.A.*