

THE EVOLUTION OF BEHAVIORS REGULATING DENSITY
AND AGE-SPECIFIC SEX RATIOS IN A
PRIMATE POPULATION

by

WOLFGANG P. J. DITTUS ¹⁾

(Office of Zoological Research, National Zoological Park, Smithsonian Institution,
Washington, D.C., U.S.A.)

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CONTENTS

I. Introduction	266
Methods	266
Definitions	267
II. The social regulation of population size and age-sex distribution	268
A. Population structure and demography of <i>M. sinica</i>	268
B. Population growth in relation to natality and mortality	269
C. Changes in population size and age-sex distribution in relation to food availability	269
D. The causes of mortality	270
E. Behaviorally induced starvation according to dominance by age and sex	270
F. Behaviorally imposed mortality in relation to mating and migration	273
G. Regulation of troop size and composition in relation to food resources, mates and non-socially imposed mortality	274
H. Conclusions	274
III. Some evolutionary considerations	275
A. The possibility of kin selection	275
B. Classical and kin selection for dominant and subordinate behaviors	277

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C. Differential mortality by age and sex as a result of reproductive strategy	279
D. Behavioral measures of parental and kin investment	280
E. Parental investment as a function of reproductive strategy	281
F. Kin investment as a function of reproductive strategy	282
G. Equal total investment per sex	283
H. Emigration of adolescent males and changes in selection pressure with age	286
I. Balance in cost: benefit of relations between adult males and other troop members	287
J. Selection for age-specific dominance	289
K. The evolution of social behavior in relation to population regulation	290
IV. Discussion	291
A. Evidence for similar phenomena in other primates	291
B. Sexual dimorphism and the evolution of sex ratios in relation to population regulation	294
Summary	296
References	297
Zusammenfassung	301

I. INTRODUCTION

New data from a long-term study of a population of toque monkeys (*Macaca s. sinica*) of Sri Lanka suggested that animals indirectly kill one another through social behaviors that involve access to resources and mates. Such mortality is not imposed randomly, but follows differences in social dominance. As dominance differs according to age, sex and kinship so do the socially imposed mortalities. The net result of these relationships is that the density as well as the age-sex distribution of the society (and hence of the population) are determined through social means and are regulated towards an equilibrium with the available food resources and nonsocially imposed mortality (DITTUS, 1977a). The occurrence of such relationships among other primates has been reviewed (DITTUS, 1979). In this paper I attempt to explain the evolution of such behaviors with the view of elucidating phenomena that may be fundamental to the social organization of other mammalian societies.

The relationships described above are basic to the development of the present topic; therefore a brief outline of the main observations and conclusions of these is presented first.

METHODS

The study area and schedule.

The study population of *M. sinica* was located within the Archaeological and Nature Sanctuary at Polonnaruwa in the dry zone of Sri Lanka. Here, approximately 450 macaques from 18 troops were investigated. The study area consists of natural semi-evergreen forest (DITTUS, 1977b). The shrub layer and some trees have been cleared in parts of the

study area to expose important archaeological ruins. The research was continuous from September 1968 to May 1972 and from March 1975 to the present. Intermittent observations were taken between May 1972 and March 1975.

Age classification.

The morphological changes with age of infants and juveniles of known birth-dates were recorded. These records were used to estimate the ages of animals of unknown birth-dates. Females were considered adult with the first pregnancy at approximately 5 years old. Males were not adult until 7 or 8 years old as judged by body size, testes, canine teeth and muscular development. Subadult males from 5 to 7 years old were as large as, or larger than adult females, but were smaller and physically less developed than adult males. Adolescent males include old juvenile males and subadult males. These males attempted mating and often strayed from the troop during the mating season and eventually migrated, whereas younger males did not. Adults were classified according to five broad categories: young, young to middle aged, middle aged, old, and senile. A host of morphological changes similar to those one might use in subjectively assessing the ages of humans formed the basis of this classification. With increasing age in the macaque there occurred erosion and tartarization of the teeth; wrinkling of the facial skin; loosening of folds of skin on the body and face, especially near the eyes, mouth and cheek pouches. The degree of facial pigmentation often intensified and facial hair and scarring became more prevalent with age. Stiffness of the joints, dull and balding pelage were frequent among old animals. A complex of such features characterized each adult age class and has been systematically presented in greater detail in DITTUS (1974). Longevity was thought to be approximately 30 years and is supported by records of captive *M. sinica* (HILL, 1937; JONES, 1962).

Behavioral observations.

All 36 and 18 animals in the two main study troops were individually identified. Each animal was followed for one or more full days and its general activity type (foraging, moving, resting, grooming, playing, *etc.*) was recorded for each minute of observation. In addition all its behavioral interactions with others were noted. At 5-minute intervals the distance from the focal animal to its nearest neighbors was estimated. Additional activity and feeding analyses were done independently. Behavioral observations were taken year round and were supplemented by observing known animals in other troops.

DEFINITIONS

The *Coefficient of relatedness* "r" expresses the proportion of genes shared between related individuals. For example, an individual is related by $r = 1/2$ to its parents or full-sibs; $r = 1/4$ to its grandparents or half-sibs; $r = 1/8$ to its full cousins.

Inclusive fitness is personal or classical fitness plus the kinship component of fitness. The latter is defined as the lifetime sum of effects (of an individual's behavior) on the fitness of relatives, with each effect weighed according to the degree of relatedness, r, of the individual affected (WEST-EBERHARD, 1975).

Kin selection has been defined by E. O. WILSON as the selection of genes due to one or more individuals favoring or disfavoring the survival and reproduction of relatives (other than offspring) who possess the same genes by common descent. See WILSON, 1973, 1975; and BROWN, 1966.

Parental investment is defined as any behavior towards an offspring that increases the chances of the offspring's survival at the cost of the parent's ability to invest in other offspring (TRIVERS, 1972).

II. THE SOCIAL REGULATION OF POPULATION SIZE AND AGE-SEX DISTRIBUTION

The original demographic, ecological and behavioral data from *M. sinica* which led to the conclusions abstracted below have been presented and discussed more fully elsewhere (DITTUS, 1975, 1977a).

A. POPULATION STRUCTURE AND DEMOGRAPHY OF *M. SINICA*

Knowledge of age and sex specific mortality schedules is fundamental to the understanding of life-history processes of organisms and thus to any attempts to speculate on certain aspects of their evolution. The theory and practical methods for life-table analyses as applied to mammalian populations have been established (DEEVEY, 1947; QUICK, 1963; CAUGHLEY, 1966). Basically, an accurate knowledge of the age and sex distributions of populations under equilibrium conditions is requisite. Mortality is calculated by assuming that the decrease in the number of individuals in successive age-sex classes is the result of mortality, once the effects of natality and of immigration and emigration have been accounted for.

TABLE 1

The age and sex structure of the population of Macaca sinica at Polonnaruwa

Age class	Age in years	Number of males	Number of females
Infant	0-1	30	21
Juvenile	1-5	83	54
Subadult	5-7	23	—
Adult male	7-30	48	—
Adult female	5-30	—	111
Total		184	186

The age and sex composition of the study population under zero net growth conditions ($R_0 = 1$) is given in Table 1. The total number of males nearly equalled that of females. There were 2.3 times as many adult females as adult males, but among the juveniles and infants there were more males than females. The sex ratio at birth was 1:1, females do not emigrate, and solitary males and all-male groups are included in the census. The ages of juveniles were known or estimated according to the morphology of juveniles of known ages. The sex ratios among the juveniles and adults therefore are not attributable to sex differences in the rates of maturation or migration; rather, they reflect differences in age-specific rates of mortality as outlined in the life table (Table 2). Among the infants and juveniles the females were subject to greater mortality than their male peers. Towards the end of the juvenile

phase male mortality surpassed that of females and reached a peak during the subadult male phase. In both sexes mortality decreased sharply with the attainment of adulthood (approximately 5 years old for females, and 7 to 8 years old for males). Throughout adulthood mortality in males was greater than in females (DITTMER, 1975).

B. POPULATION GROWTH IN RELATION TO NATALITY AND MORTALITY

The average rate of natality, over 4 years, in the population of *M. sinica* at equilibrium ($R_0 = 1$) was 0.688 infants born per adult female per year (DITTMER, 1975). Theoretically, this rate should allow a rapid net growth of the population. Although seasonal fluctuations in troop and population sizes occurred (Fig. 1), on an annual and superannual basis the net growth of 17 individual troops and of the population as a whole was zero ($R_0 = 1$). This was further confirmed by tracing the histories of 131 females over 3 to 9 years: the 33 females beginning to reproduce balanced the 33 reproducing females that died. The overall equilibrium state was achieved mainly through a balance between natality and mortality. Of all macaques born, 90% of the males and 85% of the females died prior to adulthood (*ibid.*).

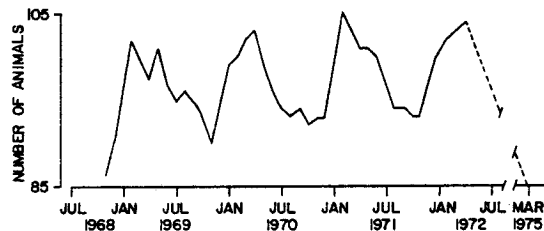


Fig. 1. Cyclical fluctuations in the total number of animals from 5 troops whose sizes were closely monitored from September 1968 to May 1972, and that were recensused in March 1975.

C. CHANGES IN POPULATION SIZE AND AGE-SEX DISTRIBUTION IN RELATION TO FOOD AVAILABILITY

The zero growth of the population of *M. sinica* occurred under long term, relatively stable ecological conditions. With a decrease in food availability, resulting mainly from a drought, population size decreased by 15.3%. This decrease was attributable to increased mortality among the juveniles, especially the youngest juveniles. Juvenile females died at statistically significantly greater rates than their male peers, and than juvenile females under equilibrium population growth conditions. In contrast, an abundant food supply stimulated population growth, and survivorship among juveniles and es-

pecially young females improved (DITTUS, 1977a). These data suggested that food supply directly influences mortality, but differently by age and sex; and that population size is closely attuned to food supply.

D. THE CAUSES OF MORTALITY

What causes the observed mortality? In the study population congenital or other disease was not apparent, and predation, mainly from feral dogs, was not a major cause of mortality. Although disease may have contributed to mortality particularly among the infants where mortality was extreme, there is no evidence to suggest that disease or predation by themselves underlie the observed pattern of mortality (Table 2). More likely disease and predation act in concert with more determinate phenomena, perhaps as arise through food related behavioral-ecological interrelationships.

TABLE 2

Life table 1) for a population of 446 Macaca s. sinica in Polonnaruwa

Age class	Age (years)	Males				Females			
		l_x	d_x	q_x	e_x	l_x	d_x	q_x	e_x
Infant	0-1	1,000	395	395	4.5	1,000	526	526	4.8
Juvenile-1	1-2	605	79	131	6.2	474	158	333	8.6
Juvenile-2	2-3.5	526	74	141	5.0	316	55	174	10.7
Juvenile-3	3.5-5								
Subadult male	5-7	303	99.5	328	5.1	—	—	—	—
Young adult male	7-10	104	7.7	74	10.5	—	—	—	—
Young adult female	5-10	—	—	—	—	152	2.8	18	16.6
Young to middle age	10-15	81	2.4	30	9.0	138	3.0	22	13.0
Middle age	15-20	69	7.6	110	5.2	123	2.8	23	9.3
Old	20-25	31	5.0	161	3.5	109	10.2	94	5.2
Senile	25-30	6	1.2	200	2.5	58	11.6	200	2.5

1) l_x refers to the number of individuals alive at age "x"; d_x refers to the number of individuals dead at age "x"; of those surviving to a particular age class, q_x refers to the proportion (per 1000) that will die annually in that age class; e_x refers to the average length of life remaining of those individuals that have survived to a given age class.

The tabulated values are averages *per annum* within each age class (see Methods) (modified from DITTUS, 1975).

E. BEHAVIORALLY INDUCED STARVATION ACCORDING TO DOMINANCE BY AGE AND SEX

Behavioral relationships were closely examined in the population of *M. sinica* under natural conditions (see Methods). An individual was considered

as dominant if it had priority of access to food, mates, and other resources. Records of agonistic behavior permitted the ordering of all animals in a troop according to a linear hierarchy of dominance. Departures from linearity occurred among some juveniles because dominance relations sometimes changed over time. A threat was defined as any behavior that caused the respondent to alter its spatial position or behavior in avoidance. The frequency of agonistic behaviors varied according to the context of activity (*e.g.*, moving, resting, playing, grooming); and 82% of all threats occurred while foraging- searching for and consuming food. Subordinate individuals, when threatened, were prevented from feeding and foods that they had found were usurped in 36% of all threat interactions (Figs 2 and 3). Since access to food is crucial to growth and survivorship, and mortality differed by age and sex, behavioral data were summarized according to the frequency of threats occurring between age-sex classes during foraging. The ratio of the respective frequencies with which individuals threatened and were threatened during foraging directly measures their relative access to contested resources. Such ratios (Table 3) indicate that adult males had greatest relative access and infant females the least. To test for the possibility of agonistic discrimination between animals of different age and sex, the observed frequencies of threats

TABLE 3

*Ratio*¹⁾ of threats given to those received per age-sex class during foraging in two different-sized troops

	Adult male	Subadult male	Adult female	Juvenile		Infant		Total
				male	female	male	female	
Number of animals in troop B	4	3	8	9	9	3	1	37
Frequency of threats given	344	28	355	355	333	52	13	1480
received	33	22	299	350	563	126	87	1480
Ratio of threats given : received	10.4	1.3	1.2	1.0	0.6	0.4	0.1	
Number of animals in troop A	2	3	4	3	3	1	2	18
Ratio of threats given : received (N = 229 threats)	8.4	2.4	1.1	0.8	0.4	0.0 ²⁾	0.3	

1) The magnitude of the ratio reflects relative access to contested food resources by age and sex. Adapted after DRRUS (1977a).

2) The infant male was a neonate mostly carried by the mother and foraging very little.

between age-sex classes during foraging were statistically tested against several progressively stronger null-hypotheses. The latter assumed random threatening between animals of different age and sex and spatial affiliation.

These tests indicated the following statistically significant results: (1) Adult males were dominant to animals of all other age-sex classes and threatened them more frequently than expected if threats had occurred randomly. (2) Dominant adult males displaced subordinate adult males, subadult males and old juvenile males to the troop's periphery away from favored feeding areas. (3) Subadult males and adult females exploited the juveniles which in turn exploited the infants. (4) Juveniles and infants were threatened more frequently by adult males than by adult females. (5) Juvenile and infant males dominated their female peers. (6) Juvenile and infant females threatened each other significantly but not their male peers. (7) Adult males and females discriminated against juvenile and infant females by exploiting them more frequently than the males of these ages. Thus, overall, female juveniles and infants were exploited for food more frequently than were the males of these ages.

Analyses of nearest-neighbor associations and of affiliative behaviors during foraging reflected the agonistic discrimination between castes, in that the subordinate infant and juvenile females were not favored by and generally did not associate with the more dominant male castes. For example, during foraging adult and older juvenile males frequently approached and hugged infant and young juvenile males. Such favoritism was never accorded young females ($N = 133$ hugs observed) (DITTUS, 1977a). In their spatial associations subordinates generally avoided the dominant animals without having to be threatened by them. Since these dominant animals fed at the richest¹⁾ food sources, the avoiding subordinates were in effect relatively deprived of these foods.

The behavioral relationships during foraging influenced the foraging efficiency of animals. Adult males were assumed to be the most efficient foragers because they spent the least amount of time (*i.e.*, effort) in foraging and the most in resting, but had the highest feeding rates and consumed the greatest proportion of foods that are high in protein and calories. By these same measures adult females were next in foraging efficiency, then juvenile males, and juvenile females were least efficient.

These differences in relative access to food apparently influenced growth

1) The "richness" of a food source was judged, for example, by the ripeness, size and density of fruit, which often differed between branches of the same tree and between different trees. It refers also to an all-or-none situation, as devouring an entire cluster of mushrooms versus eating none or only the remaining crumbs.



Fig. 2. Photograph showing an adult male (on the right) threatening and pushing an adult female away from her feeding place. This example illustrates one of a variety of behaviors used by dominant animals to exploit subordinate ones for food. In the extreme case a dominant may remove and consume food from the subordinate's cheek pouches (see Fig. 11 in DITTS, 1977a).

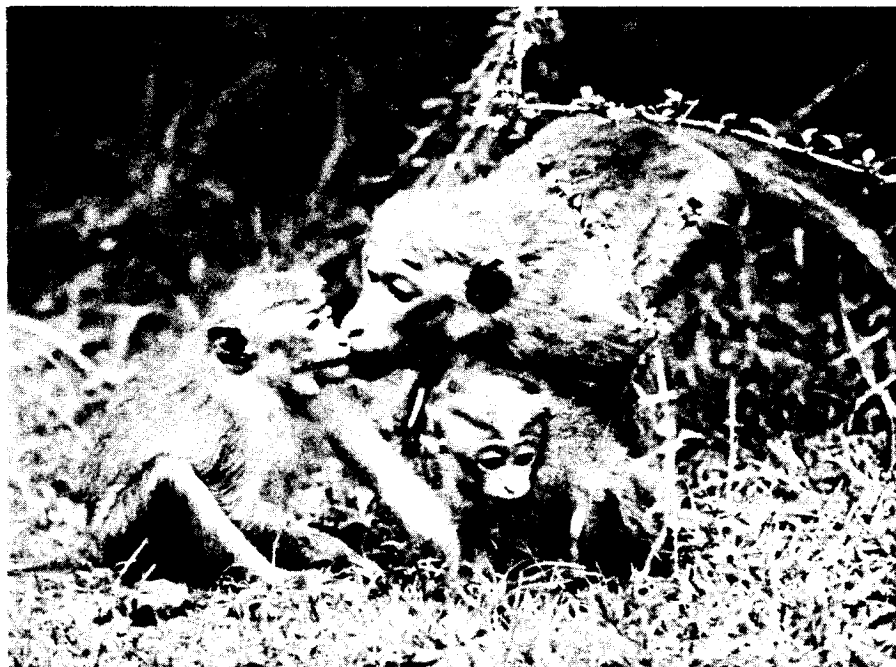


Fig. 3. Photograph showing a subadult male threatening two juveniles away from their feeding places. The instant before the photograph was taken the subadult male had sniffed at the threatened juvenile's mouth — presumably obtaining information on what the juvenile was eating. The juvenile's cheek pouches contain some food.

rates, as infant and juvenile males grew faster than their female peers (Table 4). Similarly, dominant adult males attained greater weight than subordinate ones, and a change in dominance rank was followed by one in weight (*ibid.*).

For *M. sinica* I proposed that the greater mortality manifest by the youngest animals in general, and by the females relative to the males amongst the juveniles and infants in particular, is probably the result of the much greater frequency with which they were exploited for, and prevented access to, resources. Whether death is through starvation alone, or through an agent secondary to food deprivation (*e.g.*, social stress) has not been distinguished. Behaviorally induced death through starvation has been noted, however, in a variety of macaque species studied in captivity (DITTUS, 1979).

Adult and subadult males of *M. sinica* had additional sources of mortality.

TABLE 4

Approximate differences in the growth rates between male and female juveniles (aged 0.1 to 5.5 years¹), and in the average weight of adults of Macaca sinica

	Male	Female
Number of juveniles weighed	15	8
Rate of growth in kg per year	0.590	0.407
Significance level of the difference in juvenile growth rates (t-test)		0.013
Number of adults weighed	38	37
Average weight of adults in kg	5.35	3.29
Standard deviation of average adult weight	0.70	0.33

1) Animals of known age were weighed in the field.

F. BEHAVIORALLY IMPOSED MORTALITY IN RELATION TO MATING AND MIGRATION

Migration was defined as the permanent shift of an individual to a different troop. During the mating season of *M. sinica* fighting and wounding increased markedly among adult and adolescent males that competed for mates and that migrated (DITTUS, 1977a). Migrating males were frequently attacked, had low priority of access to resources and mates and lost weight. This was most acute for adolescent males which competed with larger or adult males, and which stood less chance of establishing a dominant position in a new troop. Rates of migration were highest in adolescent males, and, on the average, all males left their natal troop prior to adulthood (DITTUS, 1975). The rigors of migration (least access to food and frequent wounding) apparently underlie the observed mortality in males. Mortality in adult males

was (1) less than in adolescent males which migrated more frequently, and (2) greater than in adult females which did not migrate or fight for mates.

G. REGULATION OF TROOP SIZE AND COMPOSITION IN RELATION TO FOOD RESOURCES, MATES AND NON-SOCIALLY IMPOSED MORTALITY

Most behaviors relating to access to resources and mates occur within the troop. Under relatively normal environmental conditions troops of *M. sinica* remained more or less the same size. With a food shortage the population decreased by 15.3%. Notably, the weighted mean decrease per troop was almost the same, 14.6% and the rank order of troop size for 17 troops did not alter significantly ($p > 0.05$) (DITTUS, 1977a). Thus, food shortage affected most troops about equally. The critical influence of the food base on troop size is further indicated by the fact that the sizes of home ranges of different-sized troops correlated positively with the number of animals per troop, but inversely with the number of food items available per individual (DITTUS, 1974). That is, for equal-sized troops, the home ranges having a low density of food plants were larger than those having a high density. Although intertroop competition in part determines the amount of food available per troop and thereby contributes to setting the upper limit to troop size (DITTUS, unpublished data), the molding of the age-sex structure is determined largely by mortality resulting from competition for resources and mates within the troop. As food resources limit troop size, the effects of competition might be alleviated through the death of other troop members. Like socially imposed mortality, that which occurs through predation or some other extrinsic means alters the age-sex composition of the troop and thereby alters the forces of competition that occur between its members.

Subordinate animals had least access to other resources, such as favored sleeping places and refugia from predators. Under conditions where these resources might be in short supply it is conceivable that competition for them may also influence survivorship. Mortality through competition for resources and mates does not, of course, preclude other kinds of socially imposed mortality. It may represent only one important manifestation of a behavioral syndrome which favors differential survivorship by age and sex; other manifestations include the direct harassment and killing of individuals (*e.g.*, infanticide).

H. CONCLUSIONS

On the basis of the data from *M. sinica*, I proposed (DITTUS, 1977a) that the age and sex specific mortalities are mostly behaviorally mediated and thus determine the age and sex distribution of the society and result in regulating

the population size in accordance with food availability and non-socially imposed mortality.

III. SOME EVOLUTIONARY CONSIDERATIONS

The relationships outlined above raise several important questions from an evolutionary standpoint. For example: (1) What is the advantage, particularly to subordinates, of behavioral relationships that impose mortality; (2) Why are adult males more aggressive during foraging than adult females; (3) Why do all males on the average emigrate from their natal troops at adolescence (DITTS, 1975); and especially (4) Why is socially imposed mortality so much greater in females than in males among juveniles and infants? Such questions might be approached by considering the possible forces of natural selection to which individuals of different age and sex may be subjected.

A. THE POSSIBILITY OF KIN SELECTION

Genealogical records of *M. sinica* indicate that troops consist of adult males and lineages of adult females (*e.g.*, Fig. 4) and their young. Records are as yet too brief (maximum of 9 years) to identify relationships between all the separate lineages of adult females within a troop. However, general genealogical predictions can be made on the basis of the following data. First, the histories of 131 adult females have been traced over periods varying between 3 and 9 years. These records indicate that females do not migrate; recruitment into the female reproductive cohort is only from daughters of adult females in the troop. Second, as in other macaques (KOFORD, 1963, 1966; KAWAMURA, 1958; SADE, 1967; KOYAMA, 1967; NORIKOSHI, 1974) dominance rank is socially inherited through the mother such that a daughter, by the time she acquires adulthood, assumes a rank just below that of her mother (DITTS,

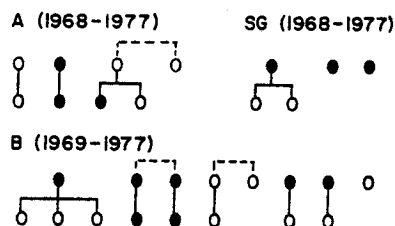


Fig. 4. Genealogical relationships are portrayed among adult females of 3 troops: A, B, and SG. Open and closed circles represent known adult females alive and dead respectively, by the end of the observation period. Vertical connections represent the mother (above) to daughter(s) (below) lineage. Solid connections show known relationships; broken line connections are assumed relationships based on conspicuous morphological and behavioral similarities. The period of observation for each troop is given in parentheses.

unpublished data); and high ranking adult females have greater reproductive success than mid or low ranking ones (Table 5). Hence, even if the coefficient of relatedness, r (see Definitions), among the founding adult females in an ancestral troop were zero, the slightest difference in reproductive success among these females and their female progeny over many generations would lead to a greater average degree of relatedness (\bar{r}) among them. And,

TABLE 5

*The reproductive success of adult females differing in social rank*¹⁾

Social rank of mother	Number of mothers	Annual birth rate per rank	Number of offspring surviving to reproduce		
			daughters	sons	total
high	15	0.750	15	4	19
mid	15	0.600	2	2	4
low	14	0.642	4	0	4

1) High ranking mothers have significantly more daughters ($p < .01$) and total offspring ($p < .01$) surviving to reproduce than mid or low ranking ones, and offspring survivorship is not proportional ($p < .03$) to differences in birth rates per maternal rank. [Kolmogorov-Smirnov One Sample two-tailed test (SIEGEL, 1956)]. Data are from 9 troops observed for periods of 3 to 9 years.

	ADULT FEMALE	INFANT AND JUVENILE FEMALE	PREADOLESCENT OR INFANT PLUS YOUNG JUVENILE MALE	ADOLESCENT MALE OR OLD JUVENILE PLUS SUBADULT MALE	ADULT MALE
RATES OF MIGRATION	DO NOT MIGRATE			ONCE EVERY 2.0 TO 3.5 YEARS	ONCE EVERY 4.2 TO 5.8 YEARS
ADULT FEMALE	CONDITION I: \bar{r} IS HIGHEST				
INFANT AND JUVENILE FEMALE					
PREADOLESCENT OR INFANT PLUS YOUNG JUVENILE MALE					
ADOLESCENT MALE OR OLD JUVENILE MALE PLUS SUBADULT					
ADULT MALE	CONDITION IV: $\bar{r} \sim 0$	CONDITION V: $\bar{r} < \bar{r}$ OF CONDITION II, DECREASES WITH INCREASING AGE OF JUVENILE	CONDITION VI: $\bar{r} < \bar{r}$ OF CONDITION V, DECREASES WITH INCREASING AGE OF ADOLESCENT	CONDITION VII: $\bar{r} \sim 0$	

Fig. 5. Relative differences in the average degree of relatedness (\bar{r}) among individuals of different age and sex classes, based on differences in their respective rates of migration, and on the knowledge that the reproductive success of adult females in a troop varies (Table 5). The symbol $\bar{r} \sim 0$ is meant to convey a minimal degree of relatedness rather than no relatedness.

juveniles and infants born in a troop should share some genes identical by descent from a common ancestral female and with the adult females (condition I, Fig. 5).

On the average all males emigrate from the maternal troop during adolescence (DIRTUS, 1975). This indicates that on the average inbreeding through matings between siblings or mother and son is prevented; and that adult males are not closely related to the adult females (condition IV) or to any of the young other than those which they themselves have sired. This probability of relatedness is further decreased due to the combined effects of migration in adult males and their sons, and the high average probability of death (85% to 90%) among any young that the adults may have sired. However, some immigrant males come from neighbouring troops. Thus, the term "unrelated" is meant only as a relative measure, and the \bar{r} between immigrant males and "unrelated" troop members is minimal. Its magnitude depends on the probability of a male returning to his maternal troop, which in turn is a function of the distance migrated and other factors. Returns of adult males to their maternal troops have not been observed.

The \bar{r} of adolescent males to females and their young is diluted because some adolescent males are unrelated immigrants. The dilution increases with age of adolescent males as the rates of migration increase with age (condition II). The \bar{r} between adult males and the young is determined solely through paternity because adult males lack ancestry in the troop, and is therefore less than the \bar{r} among females and their young. Also the probability of paternity decreases the more recently the adult male had immigrated, or the older the young. Hence, \bar{r} between adult males and young diminishes likewise (condition V). The adult males' \bar{r} with young in the troop is least with adolescent males, some of which are also immigrants (condition VI), but it is more than the \bar{r} among adult males, all of which are immigrants (condition VII). The \bar{r} between other castes is self evident in Fig. 5.

These data indicate that kin selection (see Definitions) may be operative among individuals of those age-sex classes where some degree of relatedness (r) is to be expected. They further suggest that as the coefficient of relatedness differs between individuals of different age and sex, so does the behavior and the nature of natural selection that mediates the behavioral relationships between them.

B. CLASSICAL AND KIN SELECTION FOR DOMINANT AND SUBORDINATE BEHAVIORS

The advantages of dominance to individual or classical fitness are obvious. The selective advantage of subordinate behavior to individual fitness has

been discussed by LACK (1954, 1966). Referring to birds, LACK argued that a subordinate should not contest the dominant's priority of access to resources because, by contesting, the subordinate loses valuable energy in a conflict that it would lose in any case; and the subordinate might invest this energy more profitably by searching for food in a place where (or at a time when) a contest is avoided. Reversals in dominance relations do occur, of course. Observations of macaques indicate that such reversals are rare and occur when a subordinate stands a good chance of success in its challenge. For example, young males tend not to challenge adult females singly until they have grown to the size of subadult males when they can physically overpower adult females.

Since primates compete for food, food shortage might be expected to increase aggression. However, behavioral data from wild macaques, *M. sinica* (DITTUS, unpublished data), *M. mulatta* (MORRISON & MENZEL, 1972), and baboons, *P. ursinus* (HALL, 1963), facing starvation indicated that, relative to normal conditions, aggression decreased, animals became lethargic and spatially more dispersed and spent most of the time searching for food. SOUTHWICK (1967) confirmed these field data experimentally among captive *M. mulatta*. Thus, in lieu of challenging others for access to what little food was available, these primates used their energies to search for food away from others. These primate data therefore are consistent with LACK's hypothesis, keeping in mind that subordinates are such through their inability to successfully contest dominants. In addition, a contest among *M. sinica* over a particular resource item is likely to involve a chase which exposes the contested item for consumption by a third party. By waiting unobtrusively while the dominant satiates itself, subordinates gain the opportunity of consuming at least the leftovers.

Therefore, although subordinate behavior is less beneficial to individual fitness than dominant behavior, a subordinate act, by avoiding a contest, is adaptive because it safeguards further loss of individual fitness. Conceivably, the more severe the subordinate's food deprivation, the less is its ability to improve its condition through physical contest; it is caught in a vicious circle and may survive only if sufficient food remains after the dominants have been satiated. Hence, mortality that results from the subordinate condition is likely to be a result of starvation or similar consequences of resource deprivation, and possibly social stress (*e.g.*, CHRISTIAN, 1963), rather than a result of direct fighting.

Except for immigrant males, members within a troop constitute a kinship group (Fig. 5). A subordinate act between related individuals has the advantage of contributing to the kinship component of the subordinate's

inclusive fitness (see Definitions) through the gains in fitness this act bestows upon a related beneficiary (the dominant or exploiting relative). Since a subordinate act is adaptive under classical selection alone, the loss in individual fitness through subordinate behavior need not be compensated by an equal or greater increase in inclusive fitness in order for subordinate behavior to evolve, as originally suggested by HAMILTON (1964). However, individuals should be more willing to be subordinate to a relative, especially a closely related one, because of the gains in inclusive fitness such selectivity confers.

Since a subordinate is unlikely to win in challenging a dominant, an outright challenge to a dominant relative would jeopardize the kinship component as well as the classical component of a rebellious subordinate individual's fitness. Such anti-altruistic behavior would be strongly selected against. The relative stability of the dominance hierarchy may be explained by the benefits it gives to dominants and subordinates alike; the latter making the best of a bad situation. Where subordinate behavior bestows benefits to a relative, the subordinate behavior may be considered a case of imposed altruism (WEST-EBERHARD, 1975). The evolution of altruism (subordinate behavior) by means of pure interdemic group selection is improbable for reasons outlined by MAYNARD SMITH (1964), WILLIAMS (1966) and WILSON (1973).

C. DIFFERENTIAL MORTALITY BY AGE AND SEX AS A RESULT OF REPRODUCTIVE STRATEGY

Assuming that the greater mortality of juvenile and infant females relative to the males of these ages is indeed a result of greater discrimination against them during foraging by other members of the society, several hypotheses can be presented as regards the significance and possible evolution of such behavior. As the evolution of sex ratios has been linked with mating systems (WILLSON & PIANKA, 1963), the issues to be discussed may be clarified by first considering the mating system in *M. sinica*.

The following conditions are basic to the difference in reproductive strategy between males and females: (1) Though males and females contribute equally to the ancestry of future generations (FISHER, 1958), there are 2.3 times more females than males among the reproducing adults (Table 1) such that the average adult male contributes more genes to future generations than the average adult female (Fig. 6). (2) Adult males acquire larger body size than adult females. (3) This difference starts early in life as infant and juvenile males grow faster (kg gained per year) than female peers (Table 4). That is, the growing males are likely to have greater nutritional

needs than their growing female peers. (4) Males emigrate from their maternal troop at adolescence, whereas females remain in the company of relatives all their lives (DITTUS, 1975). (5) Adolescent and especially adult males compete for mates more than adult females (DITTUS, 1977a). (6) In contrast to females, males have a prolonged adolescent phase during which they continue to grow and develop sexual maturity, and are subject to extreme mortality, partly resulting from competition for mates. (7) As adults, males continue to suffer greater mortality than adult females, primarily as a result of competition with other males for mates.

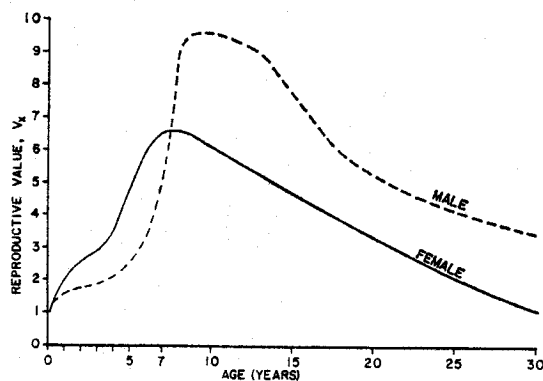


Fig. 6. The reproductive values, v_x (FISHER, 1958), indicate the average number of offspring that individuals of different age and sex will contribute to the next generation. The curves are based on life-table information (Table 2). Because the population is stable ($R_0 = 1$), the v_x of males and females at birth are unity; the average male and female is replaced only once per generation. The extreme mortality of males during adolescence lowers their v_x as infants and juveniles below those of young females, but it is compensated for in adulthood by the disparity in the adult sex ratio. Social dominance among adults influences reproductive success and may differ with age. Such differences are ignored in these curves, which, consequently are merely rough approximations.

These facts suggest that the greater reproductive success of adult males (on the average), relative to adult females, involves for them greater risks of mortality, or a shorter reproductive life, and the necessity of developing larger size and the ability to compete with other males for mates. The evolution of such differences has been attributed to intrasexual selection (MAYR, 1972).

D. BEHAVIORAL MEASURES OF PARENTAL AND KIN INVESTMENT

Parental fitness is determined by (1) the number of offspring that survive to adulthood, and by (2) the reproductive success of these surviving offspring. Therefore, any parental behavior that increases these attributes should

be selected for. If access to food increases growth and survivorship, then parents may assist growth and survivorship among their offspring by tolerating them during foraging — permitting them to share foods that the parents had found and not usurping their offsprings' food. But, if such tolerance deprives the parents of food, and thereby decreases their fitness, then it will evolve only if the gains in parental fitness through the greater survivorship of their offspring outweighs the loss in parental fitness through food deprivation or the inability to invest that same food (energy) in other offspring. Accordingly, tolerance towards offspring during foraging qualifies as a form of parental investment (see Definitions). It may be measured by the inverse of the amount that parents threaten their young.

Similarly, tolerance during foraging towards a subordinate relative would evolve only if the dominant altruist's gain in inclusive fitness (through the greater survivorship of the benefiting subordinate relative) is greater than the dominant altruist's loss in individual fitness. Such tolerance might be called "voluntary kin investment", and may be measured by the inverse of the amount of threats from dominant to subordinate relatives. Since parents are related most to their own young, parental investment should take precedence over voluntary kin investment. "Involuntary kin investment" is synonymous with imposed altruism, and the degree to which subordinates are exploited by their parents or dominant relatives reflects the amount they are forced to invest in their parents or dominant relatives. Through these relationships the degrees of threat and affiliative discrimination among castes during foraging measure, directly or inversely, the degrees of parental or kin investment (of one type) among them. Unrelated males (adult and adolescent immigrants), of course, cannot engage in kin investment, and of males only fathers may engage in parental investment.

E. PARENTAL INVESTMENT AS A FUNCTION OF REPRODUCTIVE STRATEGY

The number of animals in a troop of *M. sinica* is closely governed by the amount of food resources in the home range of the troop (DITTS, 1974). Each "vacancy" created through a death is filled, on the average, by only one other individual ($R_0 = 1$). Therefore, it would seem that the distribution of the limiting resources among individuals of different age and sex is critical to the fitness of individuals in the troop. The survival and growth rates differ for sons and daughters. Thus one might expect parental behaviors towards male and female offspring to differ also. Since parental behavior towards males ceases with male emigration at adolescence, I will first consider parental

behaviors towards males and females during the infant and juvenile phases only.

Sons grow faster and, because of mortality occurring after they emigrate from the maternal troop, are less likely to survive to reproduce and thus have lower reproductive values than daughters. After sons emigrate their survivorship and growth are out of parental control. However, parents that cater to their sons' growth needs, and that "anticipate" impending mortality among their sons and offset it before the sons emigrate, stand to gain greater fitness through sons than parents that do not invest in this manner. Parents may increase the chances that at least some sons survive to reproduce by producing many large-sized sons up to the age of emigration. Thus during the infant and juvenile phases it costs more (in terms of investment or loss of parental fitness) to assure the survival and development of an average son to mean reproductive age and condition, than it does to assure this for an average daughter. Parents, however, are compensated for this greater cost of sons (in terms of fitness) through the greater reproductive success of adult sons (see below). Parents that were to invest equally per individual son as per individual daughter, or more in a daughter (during the infant and juvenile phases) would produce a disproportionate number of adult daughters. Such an aberrant sex ratio among their reproducing progeny would tend not to maximize the individual fitness of parents. ¹⁾

Among several species of macaque, *M. mulatta*, *M. fascicularis*, *M. radiata* (VALERIO *et al.*, 1969, 1971) and *M. cyclopsis* (PENG *et al.*, 1973), males weigh more than females at birth. Such maternal investment gives sons a "head start" over daughters and may be true also of *M. sinica*. It would aid young males to acquire dominance over female peers thus enabling young males to more easily exploit young females for food, and thus to acquire the larger size necessary for male survival and reproductive success.

F. KIN INVESTMENT AS A FUNCTION OF REPRODUCTIVE STRATEGY

Adult females and the young in the troop are related (Fig. 5). Therefore, the behaviors among them are influenced by the effects of these behaviors upon the kinship components of the relatives' respective inclusive fitnesses. With the exception of typically parental behaviors (*e.g.*, nursing), the

1) This conclusion rests on the theorem that individuals of a mating pair will maximize their fitnesses if the pair produces males and females in such a ratio that the product of the numbers of each sex successfully raised to reproductive age is maximized within the limits set by its physiological capabilities (see MACARTHUR, 1965; EMLEN, 1968a, 1968b). The starting point of my argument assumes that the observed adult sex ratio (or the concomitant degree of sexual dimorphism achieved through intrasexual selection, — see below) is approximately the outcome of past selection.

behavioral relationships involving access to resources that occur between dominant parents and their subordinate young, are comparable to those occurring between other dominant and subordinate relatives. The r between full sibs is the same as that between parents and their young; and, although the r among other kin is less, the relationship whereby a relative gains greater inclusive fitness by investing more per male kin than per female kin of the same age and r (during the infant and juvenile phases), is comparable to (but less than) the gains in fitness through parental investment in male versus female young. In addition, however, the survival and reproductive success of related young males who emigrate can only increase a female's inclusive fitness, whereas the survival of related young females, particularly to breeding age, continues to present a direct source of competition for herself and her own sons and daughters to whom she is most related. Thus, the survival of female relatives eventually is likely to decrease her fitness more than the survival of male relatives. The behavioral discrimination during foraging that a female shows against young females in favor of young males therefore may be explained by the gains this behavior bestows: first, to her individual fitness through the greater survival of young sons versus young daughters; and second, to the kinship component of her inclusive fitness by the greater survival of male versus female relatives during the infant and juvenile phases.

Similarly, young males and females stand to contribute more to the kinship component of their inclusive fitnesses by exploiting female relatives more than male relatives (of the same age and r).

G. EQUAL TOTAL INVESTMENT PER SEX

Although parental and kin investment is greater in males than in females during the infant and juvenile phases, investment in males ceases at adolescence when they emigrate from the maternal troop. Females, on the other hand, remain in the troop through life and presumably they benefit from this association to the detriment of the mother and other relatives for longer than do the males. This detriment to others occurs because the females compete for and thereby deprive others of limiting resources in the troop. Also, to the cost of raising offspring or kin (in terms of loss of fitness to parents or kin) must be added the cost of raising those that died (LEIGH, 1970). As more females than males die during the infant and juvenile phases, the cost of "false starts" initially is greater in females than in males, but after male emigration this cost is greater in males. Total investment between the sexes among progeny and relatives can be assessed more accurately as follows.

Assuming that parental and kin investment is proportional to growth and

survival of progeny or kin, growth and survival may be used as measures of such investment. Metabolic weight expressed as $\text{kg}^{0.75}$ is proportional to basic metabolic rate and food requirements (KLEIBER, 1975). Thus, instead of weight per se, the relative metabolic weights ($\text{kg}^{0.75}$) of progeny (or kin) might be more accurate indicators of the differences in energy that parents and relatives must invest in the growth needs of male versus female progeny (or kin). Cumulative survivorship (Fig. 7) and the cumulative product of survivorship and metabolic weight ($l_x \times \text{age specific metabolic weight} - \text{kg}^{0.75}$) (Fig. 8) are plotted against age for males and females.

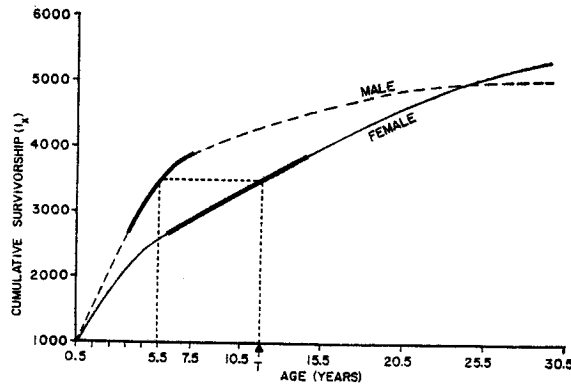


Fig. 7. The cumulative number of males and females surviving with increasing age. Differences in cumulative l_x between males and females reflect differences in the amount of investment in them by their parents and kin. The marked region of the male curve corresponds to the age range during which adolescent males emigrate. The region of the female curve which is equivalent, in terms of cumulative l_x , to the marked region of the male curve, is also marked. The median age at which males leave the maternal troop (approximately 5.5 years old) corresponds, in terms of cumulative l_x , to the mean generation length, $T = 11.84$ years, of females.

The age range and median age at which males emigrate is demarcated and indicates the age at which parental and kin investment in males ceases. The ages of females which correspond to an investment equivalent to that in males can be read from these curves. They indicate that the total investment in males up to the approximate median age (5.5 years) at which investment ceases, corresponds to the mean generation length ($T = 11.84$ years) of the female cohort. The latter was derived independently from life table information (Table 2). Thus, total parental and kin investment in male and female progeny is equal per generation, but for females it extends through the average duration of the generation, whereas in males it is concentrated in a much shorter time span, ceasing at emigration. Consequently investment in males, prior to emigration, is greater than in females of the same ages.

Equal total investment in male and female progeny or generations is consistent with genetical models originally suggested by FISHER (1958)¹ and developed by others (LEIGH, 1970; BODMER & EDWARDS, 1960; KOLMAN, 1960; EMLEN, 1968a, 1968b, 1973). These authors also concluded, however, that differential mortality by sex occurring after the end of parental care cannot affect sex ratios among progeny before the end of parental care. This

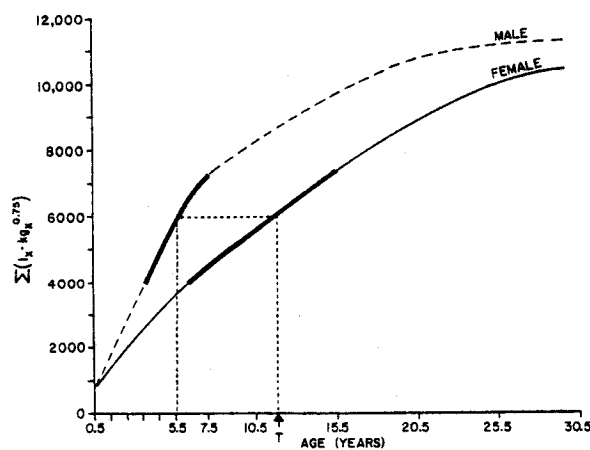


Fig. 8. The cumulative metabolic weight ($\text{kg } 0.75$) of the male and female cohorts with increasing age. The curves roughly reflect the relative amount of energy or resources that parents and kin invest in the survival and growth of their male and female progeny or kin. The marked regions of the curves reflect the same relationships as in Fig. 6, but measured in terms of cumulative metabolic weight.

conclusion needs to be refined because macaques appear to modify their investment in "anticipation" of differential mortality by sex occurring after the period of parental care in males. Thus, parents and kin invest in their young so as to maximize the chances of the young's survival to at least mean reproductive age and attainment of attributes necessary for at least mean reproductive success. MACARTHUR's model (1965) likewise must be modified to read as follows: natural selection will favor that composition of males to females of mean reproductive age which maximizes the product of their reproductive values at these ages respectively. Recent genetical models by EMLEN (1968a, 1968b, 1973) lead to the same conclusion.

"Mean reproductive age" is, of course, an abstraction representing a range of adult ages in the macaque, such that the average outcome of equal invest-

1) FISHER's (1958) arguments apply to diploid organisms in the absence of inbreeding. For the effects of sex-linkage and inbreeding on the parent's preferred sex ratio see HAMILTON (1967). Such effects are ignored in the present considerations.

ment in males and females is (1) equal total survivorship of males and females (Fig. 7), and (2) equal total energy requirements, and thus, presumably, equal total use of contested resources by the male and female cohorts (Fig. 8). Theoretically the end points of the male and female curves in Figures 7 and 8 should coincide. In Figure 7, cumulative female survivorship is slightly greater than that of males because there were 203 females to 192 males in the population on which these curves are founded. Average life expectancies (e_x) of male and female infants approach equality at birth, that is, the life expectancies of the male and female cohorts are equal (QUICK, 1963).

In Figure 8 weight ($\text{kg}^{0.75}$) alone was used to assess relative energy needs. This may underestimate the relative energy needs of females because of sex differences in physiology and behavior. For example, (1) females of all ages expend more time (*i.e.*, energy) than their male peers in fulfilling their nutritional requirements (DITTUS, 1977a) and (2) the physiological demands of reproduction are probably greater in females, although this may be partly counterbalanced by the greater activity males expend in mate competition, the latter including learning to compete, as in play fighting among juvenile males.

The male and female cohorts contribute equally to the ancestry of future generations (FISHER, 1958); thus, total fitness gained through male progeny or kin equals that through female progeny or kin. This means that the disparity in reproductive success between male and female adult individuals must be balanced overall by the greater number of female progeny and kin surviving to reproduce, or by their longer reproductive lives. Total parental and kin investment in male and female progeny or kin is also equal; hence, the overall ratio of cost (loss of fitness) to benefits (gain in individual and inclusive fitness) of parental and kin investments, is equal for male and female progeny or kin, individually and collectively.

H. EMIGRATION OF ADOLESCENT MALES AND CHANGES IN SELECTION PRESSURE WITH AGE

It is logical that a young male should be progressively less tolerated as he grows older. First, in the average troop adult males are less likely to have sired old juveniles and subadults than young ones (Fig. 5). Such unrelated young males compete for resources with the adult males and particularly with those juveniles that the adult males did sire and that are subject to exploitation because of their lesser ages or sizes. Second, as a young male attains puberty, he poses a direct threat to the individual fitness of adult males, even to his father, if the young male (or son) successfully mates to the exclusion of other adult males (or the father). The greater threat and fewer affiliative behaviors

that adult males display towards older juveniles and especially the subadult males in reference to both food and mates (DITTMUS, 1977a) is explicable on the basis of gains in individual fitness that such behavior is likely to confer on adult males. Third, as the young male grows his physical prowess enables him to exploit his mother and younger siblings and relatives for food resources. In effect this would be equivalent to enforcing greater parental and kin investment in related adolescent males. Such investment cannot exceed that "allotted" to the mean generation length of females (Figs 7 and 8) without disrupting the adult sex ratio of the next generation. It would therefore not maximize the fitness of parents or kin and explains why males must emigrate at adolescence. From the point of view of an adolescent male, his access to mates and favored resources is hindered especially by adult males, [who are likely to be unrelated to the adolescent (Fig. 5)], such that his individual fitness is in jeopardy anyway. By emigrating the adolescent male at least safeguards the kinship component of his inclusive fitness, and gains the opportunity of improving the classical component of his fitness by altering his social setting.

When adolescent males emigrate from the maternal troop, any tolerance that was shown them is lost as they compete directly with unrelated adolescent and adult males for resources and mates. Unless they emigrate in the company of related males (which would be to their benefit), they are subject to behaviors that most probably evolved under classical selection. The high rates of mortality in adolescent males suggest that the behavioral and anatomical features that enable males to dominate others and that develop most during adolescence (DITTMUS, 1977a) are strongly selected for.

I. BALANCE IN COST: BENEFIT OF RELATIONS BETWEEN ADULT MALES AND OTHER TROOP MEMBERS

Foraging strategy may relate to reproductive strategy so as to balance the cost: benefit in fitness of behavioral and morphological relations between adult males and other troop members. Thus, large size and aggressiveness in males may be essential not only in competition with other males, but also with unrelated females. A newly immigrated male must find food in an unknown home range. Usurping food from animals that have located food is a sure way of surmounting this handicap. Indeed, such behavior by dominant males was frequently observed when food was spatially dispersed and finding it required much searching. The most dominant males often did not search for food at all, but instead remained on the look-out for animals that began feeding and then rushed there to steal their foods. This "parasitic" relationship is reflected by the frequency with which adult males threatened

and maintained a close spatial association with adult females during foraging (DITTUS, 1977a). Females theoretically should (and sometimes do) resist such domination of themselves and their young, especially as they are unrelated to the dominant male immigrants. Hence, male physical superiority and a behavioral inclination to impose physical abuse in order to gain access to food are most advantageous when this superiority is so much greater as to guarantee "no contest".

By being exploited adult females constitute an indirect potential food source to dominant males. This helps explain why males remain with the troop year round and not just during the mating season; other reasons being to protect their offspring against predation and exploitation by others, and to benefit from a variety of established social relationships, as, for example, familiarity with female mates or male supporters in agonistic encounters, and to benefit from familiarity with the habitat.

The reproductive strategy whereby adult females are smaller sized than adult males may impose certain constraints on other aspects of female life history. For example, it suggests that females do not migrate because they are not physically equipped to dominate others through physical coercion; that is, to make a living outside their own kingroup and home range. Instead, they remain in the same troop (home range) all their lives and presumably accumulate an intimate knowledge of resource availability in that home range. Such a knowledge would be especially adaptive in view of their being exploited for food resources, and would be strongly selected for prior to adulthood when they are most frequently supplanted from the food sources they may have found, and when their mortality is highest.

Several benefits of associating with kin and adult males compensate the females for their altruistic behavior. First, adult males protect females and their young from predators, other troops and marauding males. Second, by forcing subadult males and subordinate adult males to remain peripheral to the troop, dominant males are in effect protecting the females and their young from resource exploitation by these peripheral males. Third, females benefit from the altruistic behavior of relatives in the troop.

Adult males more frequently exercise their priority of access to resources than do the adult females (*ibid.*). There may be several reasons for this. First, adult males on the average are less related to the young in the troop than are the adult females (Fig. 5), and unlike the females they incur no loss of inclusive fitness by exploiting unrelated young. Such exploitation would be most advantageous to recently immigrated males who have not sired young in the troop. In fact, by imposing mortality on infants sired by other males, newly immigrated males may "free" the mother for mating and impregnation

with their own young.¹⁾ This behavior would effectively increase their own fitness at the expense of the females and other males. The killing of infants by new male leaders in troops of a variety of macaques, baboons and redbellied monkeys (ANGST & THOMMEN, 1977; STRUHSAKER, 1977) and of langurs, *Presbytis entellus* (SUGIYAMA, 1967; HRDY, 1974, 1976; MOHNOT, 1971) and *P. senex* (RUDRAN, 1973), has been similarly interpreted. Such infant killing may have additional benefits for an immigrant male's fitness, however, given that troop size is resource limited. By killing unrelated young, either indirectly through resource usurpation or directly through infanticide, a newly immigrated male (a) reduces future food competitors for himself, and especially (b) culls unrelated juveniles which, by virtue of being older than his own (as yet unborn) young, would dominate or exploit his young. Second, adult males have greater energy requirements than smaller troop members, and priority of access to food enables them to forage more efficiently; they feed at higher rates and spend less time in foraging (DITTUS, 1977a). The time and energy saved frees adult males for other activities such as vigilance and troop defense which benefit other troop members. The degree to which females and their young are exploited for resources by adult males reflects the cost (in terms of loss of fitness) they "pay" for the benefits of protection from predators and other troops or males.

J. SELECTION FOR AGE-SPECIFIC DOMINANCE

A tendency for immature offspring to dominate (exploit) their parents would be rapidly selected against particularly if such coerced investment impaired the parents' ability to invest in other offspring, and if this loss of fitness outweighed the gains in fitness won through the survival of the dominating offspring. Adults, with high reproductive values (Fig. 6), therefore dominate their non-reproducing offspring and kin and exercise some control over their growth and survivorship.

The reproductive values of infants and juveniles increase with age, and parents and kin have invested cumulatively more (Figs 7 and 8) in old juveniles than in young ones (of the same sex and r). Hence, parents and kin stand to lose more of their potential for contributing to the ancestry of future generations if an old, rather than a young juvenile (of the same sex and r) were to die. The cost: benefit in fitness of investing by age must be

1) Females, whose unweaned infants die; subsequently exhibit estrous behavior and bear new infants sooner than if their first infants had continued to live: *M. sinica* (DITTUS, unpublished data); *M. fuscata* (TANAKA *et al.*, 1970); *M. fascicularis* (ANGST & THOMMEN, 1977); *Presbytis entellus* (SUGIYAMA, 1967; HRDY, 1974); *Cercopithecus ascanius* (STRUHSAKER, 1977).

weighed against the juvenile's sex and its r to the investor: obviously a parent would gain more fitness by investing in its own infant than it would by investing in an older but distantly related juvenile. The fact that older juveniles generally dominate younger ones may be explained partly by the benefits this relationship bestows upon the fitnesses of their parents and kin. Also, of course, old juveniles, by virtue of their larger sizes, are able to coerce younger ones, and such dominance contributes directly to the individual fitness of older juveniles.

The relatively low reproductive values of very old individuals (Fig. 6) suggests that their fitness might be served best if they were not to dominate their adult offspring, which, because of their youth, have higher reproductive values.

K. THE EVOLUTION OF SOCIAL BEHAVIOR IN RELATION TO POPULATION REGULATION

In all of the foregoing discussions it is implicit that individual growth and survivorship are not a function solely of social behavior, but also of the environmental conditions, such that the influence of behavior on growth and survivorship will vary according to the availability of contested resources (*e.g.*, food). It is assumed that there is an inverse relation between the cost (in terms of loss of fitness) of extracting energy from the environment (*e.g.*, finding food) or of conserving it (*e.g.*, avoiding predators) and the energy available for growth and reproduction, as in parental and kin investment.

Under conditions of food shortage ($R_0 < 1$), where a loss of fitness, by at least some individuals, is inevitable because of physical deterioration or death resulting from insufficient food, one might expect individuals to behave in a manner which minimizes their loss of fitness. Thus, parents and kin may curtail investment in their offspring and kin and utilize the energy so conserved to safeguard their own ability to reproduce at a time when environmental conditions improve. Parents or kin would lose the least fitness if the curtailment of such investment were (a) in younger rather than in older offspring or kin of the same sex and r (see preceding section), and (b) in young females rather than males of the same age and r (see sections III, E and F). The increased mortality observed among juveniles in general, but especially among the youngest juveniles and the infants, and the greater increase in mortality observed among the female juveniles, under conditions of food shortage (DITTUS, 1977a; STRUHSACKER, 1976) are consistent with these interpretations.

Under conditions of food surplus where the cost of extracting energy and nutrition from the environment conceivably is less than under conditions of

equilibrium or of food shortage, one might expect the cost of parental and kin investment to be met more readily. Consequently, the growth and survivorship among infants, young juveniles and female juveniles, may improve. Such changes in survivorship by age and sex are in fact observed when food is in surplus (DITTUS, 1975, 1977a).

I propose that the regulation of population size and age-sex distribution is an outcome of classical and kin selected (aggressive and affiliative) behaviors that (1) influence growth rates and impose mortality by determining access to vital resources and estrous females differentially by age, sex and the degree of relatedness, r ; (2) function to maximize the classical fitness of unrelated animals and the inclusive fitness of related troop members in accordance with reproductive strategy and the availability of limiting resources; and (3) result in bringing the troop size and population size into equilibrium with the available food resources and non-socially imposed mortality.

IV. DISCUSSION

A. EVIDENCE FOR SIMILAR PHENOMENA IN OTHER PRIMATES

Differences in the reproductive strategies between males and females that involve adult males larger than females, male emigration and competition for estrous females, and a prevalence of females among the adults are common for nearly all Cercopithecinae (EISENBERG *et al.*, 1972) and many other mammals (EISENBERG, 1966). Also, the basic social unit of most Cercopithecinae consists of several adult females, one or more adult males and their progeny (EISENBERG *et al.*, 1972). In some macaques close genealogical relationships between group members (excepting immigrant males) is evident (KAWAMURA, 1958; SADE, 1967; KOYAMA, 1967; NORIKOSHI, 1974) and the possibility of kin selection has been suggested (KURLAND, 1977). Additional demographic, ecological and behavioral data that are necessary to test the present hypotheses in other species are rare and incomplete for any one species. Such comparative data as do exist have been reviewed more extensively elsewhere (DITTUS, 1979). The following synopsis outlines our current state of knowledge, and indicates where additional research may be desirable.

Except for the population of *M. sinica*, no other primate population has been subjected to life-table analyses, and only a few populations have been adequately censused to allow some demographic predictions. The latter include populations of: macaques *Macaca mulatta*, *M. fuscata*, *M. radiata*; baboons *Papio cynocephalus*, *P. anubis*; vervet monkeys *Cercopithecus aethiops*; and South American howler monkeys *Alouatta seniculus* and *A. caraya*. Census data from these species (see DITTUS, 1979 for original data and references)

suggest a pattern of age-sex specific mortality similar to that in *M. sinica* (Table 1). In all of these species adult males achieve larger size than adult females; where known, infant and juvenile males grow faster than their female peers — *M. mulatta* (GAVAN & HUTCHINSON, 1973), *M. sylvana* (ROBERTS, 1978).

Populations of *Macaca mulatta* (KOFORD, 1965) and *M. fuscata* (ITANI, 1975) have grown 9% to 16% annually when provisioned with food by man. In contrast, wild populations of *Cercopithecus aethiops* (STRUHSAKER, 1973, 1976; GALAT & GALAT-LUONG, 1977) and of *Papio cynocephalus* (HAUSFATER, 1975) have diminished in size when their natural food supply was destroyed. The decrease of *C. aethiops* populations was due to increased mortality especially among the youngest or most subordinate juveniles (STRUHSAKER, 1976); and the increased mortality in the diminishing population of *C. aethiops* studied by GALAT & GALAT-LUONG (1977) was attributed to malnutrition. Food supply, rather than predation, appears to govern the net growth rate of primate populations in general (see DITTUS, 1979).

The food related behavioral control of population size, or composition, has not been adequately studied. But, an important relationship between food, dominance and mortality is indicated: (1) Dominance hierarchies are described most reliably on the basis of priority of access to food among many Cercopithecinae (BERNSTEIN & SHARPE, 1966; RICHARDS, 1974; FARRIS & HAUDE, 1976), and *Alouatta* (GLANDER, 1975). (2) In SOUTHWICK's (1967) experimental study of aggression in *Macaca mulatta* dominant monkeys prevented subordinate ones from feeding with the result that the food intake of each monkey was directly related to its position in the dominance hierarchy, the most subordinate monkeys dying from starvation. (3) Similar behaviorally induced starvation and death has been noted among captive *M. mulatta*, *M. fuscata*, *M. speciosa* (BERTRAND, 1969) and among *M. nemestrina* (BERNSTEIN, 1969).

It follows that such hierarchically mediated mortality should differ by age and sex if the dominance relationships so differ. Adult males are dominant to all other age-sex classes, the youngest being the most subordinate, in the following species: *M. mulatta* (SOUTHWICK, 1969), *M. radiata* (SUGIYAMA, 1971), *Papio anubis* (ROWELL, 1967), *P. ursinus* (SAAYMAN, 1971), *Cercopithecus aethiops* (STRUHSAKER, 1967), and *Alouatta palliata* (GLANDER, 1975). Dominant males supplant subordinate ones to the troop's periphery in these species. Behavioral discrimination against young females is indicated as follows: (1) Among juveniles and infants, males dominate their female peers in the three species where such a distinction has been attempted: *M. mulatta* (MØLLER *et al.*, 1968), *M. fuscata* (NORIKOSHI, 1974) and *P.*

cynocephalus (HAUSFATER, 1975). (2) Among captive *Macaca fascicularis*, dominant adult males attacked and killed infant and juvenile females more frequently than the males (ANGST & THOMMEN, 1977). (3) Such sex discrimination may begin even before birth. Among captive *M. nemestrina* pregnant females carrying female fetuses were attacked and bitten by other group members more frequently than females carrying male fetuses (SACKET *et al.*, 1975). This discrimination occurred only during the latter half of the pregnancy term when male hormones from the fetus begin circulating in the mother's blood — presumably communicating her infant's sex to other group members.

DRICKAMER (1974) reports that infant survivorship was greater for high ranking mothers than for low ranking ones in a food provisioned and growing population of *Macaca mulatta*.

Wounding and mortality resulting from fighting among males of *M. mulatta* increased during the mating season (*e.g.*, BOELKINS & WILSON, 1972; LINDBURG, 1971). Fighting for mates also occurs among males of *Alouatta seniculus* (NEVILLE, 1972) and *A. palliata* (GLANDER, 1975). Male migration during the mating season has been witnessed in *M. mulatta* (*e.g.*, KOFORD, 1965; LINDBURG, 1969), *M. fuscata* (*e.g.*, KAWANAKA, 1973), *P. anubis* (ROWELL, 1969), *P. cynocephalus* (ALTMANN & ALTMANN, 1970), *C. aethiops* (STRUHSAKER, 1973) and others. Where distinguished the rates of migration were highest among subadult males: *M. fuscata* (KAWAI & YOSHIBA, 1968), and *M. mulatta* (WILSON & BOELKINS, 1970). Mortality has not been linked with migration in these studies. However, in experiments simulating migration, strange monkeys that were introduced to established groups were much attacked and sometimes killed by the group members among several macaque species (BERTRAND, 1969; SOUTHWICK, 1969) and baboons (HALL, 1964).

In conclusion, where the demographic and behavioral data exist in sufficient detail, they are in accord with those pertaining to *M. sinica*. Collectively, these data indicate the existence of social behaviors which predispose individuals to grow, survive and reproduce differently according to their age, sex and genealogy, and according to the environmental conditions. Such behaviors involve competition for resources and mates which may lead to the direct killing of individuals.

This evidence, together with the similarities in mating system and social organization between *M. sinica* and many other primates suggests a broader phylogenetic relevance of the observations and hypotheses presented on the basis of data from *M. sinica*.

B. SEXUAL DIMORPHISM AND THE EVOLUTION OF SEX RATIOS IN RELATION TO POPULATION REGULATION

As the hypotheses presented herein concern the selection for behaviors that adjust demography in relation to environmental conditions and reproductive strategy, the hypotheses might be useful in predicting changes in behavior, and hence in demography among species where reproductive strategy and environmental conditions differ from those in *M. sinica*.

The view adopted here is that the larger size of males, among adults, is predominantly the result of intrasexual selection, or, of competition between males for mates. But, other vital activities, such as foraging or avoiding predators, will also impose certain morphological constraints. For example, some anatomical and behavioral features are better suited than others for efficient feeding at the terminal twigs of large branches (GRAND, 1972). The smaller sizes, and lesser size differences by sex, evident among the more arboreal species of Cercopithecinae may well reflect morphological constraints imposed by the need to forage efficiently in trees. Thus, at least three factors may influence the degree of sexual dimorphism: (1) intrasexual selection; (2) the type of environment; and (3) other selective pressures that evolve a species to exploit its niche efficiently, and, that may oppose or limit the effects of sexual selection.

A given degree of sexual dimorphism, and mating strategy, in turn, may delimit other aspects of male and female life histories, as manifest behaviorally and demographically. For example, the vertical (ordinate) differences between the male and female curves in Figures 7 and 8 reflect the degree of sexual dimorphism in behavior and anatomy. Conceivably, in species where sexual dimorphism is less than in *M. sinica*, the vertical separation of the male and female curves would be less, and in almost monomorphic species the curves might nearly coincide. In the latter case one might expect little difference in parental and kin investment behaviors towards male and female offspring and relatives, females as well as males might emigrate from the natal troop, and differences in maturation and mortality by sex might be less marked than in *M. sinica* such that the sex ratio at all ages would tend towards equality. That is, the life-histories for males and females might be very similar in monomorphic species. Indeed, the nearly monomorphic lemurs *Lemur catta* and *Propithecus verreauxi* (JOLLY, 1966), gibbons *Hylobates lar* (CARPENTER, 1940; ELLEFSON, 1974) and siamang *Symphalangus syndactylus* (CHIVERS, 1975), show a common pattern whereby, relative to the more dimorphic macaques: dominance behaviors in general are less prevalent; adult males are co-dominant with adult females; behavioral differences by sex in general are reduced; and, although sex ratios among the juveniles are un-

known, the adult sex ratios are equal (see reviews by CROOK, 1972; KLEIMAN, 1977). Also, emigration from the natal troop has been suggested (though not yet confirmed) for females as well as males of *Hylobates lar*, as a process whereby new breeding pairs are formed (CARPENTER, 1940; ELLEFSON, 1974).

In species such as baboons where sexual dimorphism is greater than in *M. sinica*, the vertical separation of the male and female curves in Figures 7 and 8 would be greater. Under resource limitation fitness is maximized if parental and kin investment is equal in male and female progeny and kin (an extension of the original argument by FISHER, 1958; see section III, G). Hence, increasing investment in males for their development to a larger size ought to be compensated for by reducing investment in other ways, such as decreasing the number of males. That is, an increase in adult male size should be accompanied by an adult sex ratio favoring fewer males; and, behaviorally, males might emigrate from their natal troops at a relatively earlier age, and suffer greater mortality (relative to females) in migration and mate competition than males of less dimorphic species. Field data, in so far as they are available, support these predictions. In the highly dimorphic patas monkeys *Erythrocebus patas* the weight of adult males is more than twice that of adult females, males grow faster than females among juveniles, and the adult sex ratio is extreme, averaging eight adult females per adult male (after data in HALL, 1965; STRUHSAKER & GARTLAN, 1970).

The above argument rests on the assumption that limiting resources are utilized equally by the male and female cohorts. To some extent males of highly dimorphic species may be preadapted, however, to utilize their attributes (such as large body size, canine teeth, and highly developed fighting ability) which originally resulted from intrasexual selection, to circumvent these energy constraints by exploiting a niche which is not exploitable by other members of the species. A case in point might be the highly dimorphic baboons where predation on other vertebrates is almost exclusively the domain of large sized adult males (DEVORE & WASHBURN, 1963; ALTMANN & ALTMANN, 1970). The carrying capacity of the environment has increased, but only for that segment of the population (adult males) which is capable of exploiting the additional potential resource. Under such conditions the sex ratio among adults may favor more males than if niche utilization were independent of phenotypic differences by age and sex.

The forces of natural selection acting on social individuals living in complex environments are probably many. Other influences, not considered here, might include the distribution and nature of food resources, the species' trophic specializations and phylogenetic history — all of which bear on the manner in which individuals interact with one another and the environment.

SUMMARY

Adult females within a macaque troop are related to one another and to all infants and juveniles. Thus, the evolution of social behaviors that impose mortality differentially by age and sex is interpreted in light of classical and kin selection. Parental and kin investment are defined and measured by the degree to which dominant relatives tolerate (closely associate with but do not exploit) subordinate relatives during foraging; and, by the degree to which subordinate relatives are exploited for resources by their dominant relatives. Sex differences in mortality among juveniles and infants are the outcome of differences in parental and kin investments which are geared to maximize fitness according to sex differences in reproductive strategy. Relative to females, males grow faster during youth, and acquire larger adult size and a greater ability to compete for mates. Males also suffer higher mortality as adults and particularly during adolescence when males emigrate from the maternal troop and when the attributes necessary for male reproductive success develop most. Such differences probably evolved through intrasexual selection. Investment involves offsetting mortality occurring in males after they emigrate from the maternal troop by investing in them heavily prior to their emigration so as to maximize their chances of survival and development to reproductive age and state. This is achieved at the expense of investment in their infant and juvenile female peers, which consequently suffer greater mortality than do infant and juvenile males. Males, however, must emigrate at adolescence to prevent additional investment in them at the further expense of related female peers. By emigrating, adolescent males safeguard the kinship component of their inclusive fitness and gain an opportunity to improve their otherwise jeopardized individual fitness in a new social setting. The relatively low investment in females during the infant and juvenile period is balanced or compensated to equal that in males by continued investment in them through adulthood, as females do not emigrate from their maternal troop. Thus, total investment in the sexes is equal and parents and kin gain equal fitness through male and female progeny and kin. The male and female cohorts utilize contested resources equally. Altruistic and exploitative behavioral relations between related or unrelated males and females are explained on the basis of a balance between cost and benefit in fitness (classical and inclusive) that these behavioral relations confer.

Relative to equilibrium conditions ($R_0 = 1$), when food supply decreases ($R_0 < 1$), mortality increases among the infants and youngest juveniles, and among female relative to male juveniles; whereas under food surplus ($R_0 > 1$) survivorship among these animals improves. Thus, when the availability of limiting resources changes, the effects of parental and kin investments on growth and survivorship, and probably their nature, change as well, so as to maximize fitness under the new conditions.

I propose that the regulation of population size and age-sex distribution is an outcome of classical and kin selected (aggressive and affiliative) behaviors that (1) influence growth rates and impose mortality by determining access to vital resources and estrous females differentially by age, sex and the degree of relatedness, r ; (2) function to maximize the classical fitness of unrelated animals and the inclusive fitness of related troop members in accordance with reproductive strategy and the availability of limiting resources; and (3) results in bringing the troop size and population size into equilibrium with the availability of food resources and non-socially imposed mortality.

Though scant, data from other species are in accord with those from *M. sinica*, thereby suggesting a broader relevance of the hypotheses and conclusions set forth in this paper. For example, as parental and kin investment are geared to maximize fitness according to the degree of sexual dimorphism, it is reasonable to expect parental and kin investment behaviors, and thence the age-specific sex ratios, to vary according to the magnitude of the difference in sexual dimorphism in size and mating strategy. A monomorphic mating system (as in lemurs and gibbons) predictably would require a minimum of difference in parental and kin investment behaviors by sex, and sex ratios should therefore tend forwards

equality at all ages. But, in highly dimorphic species (*e.g.*, patas monkeys and baboons) differences in parental and kin investment in male and female offspring and kin would be accentuated, such that the need to develop large adult male size, for example, might be compensated for by decreasing the number of males among adults. Comparative data support these implications. Other selective pressures, concerning for example, trophic adaptations, might limit the effects of intrasexual selection on the degree of sexual dimorphism, and in this indirect way influence investment behaviors and age-specific sex ratios. Similarly, niche adaptations that are specific to one age or sex only may alter the age and sex ratios in favor of the age-sex class exclusively benefiting from the additionally exploitable resource. Thus, reproductive strategies, trophic and similar life-sustaining adaptations and the availability of limiting resources influence social behaviors which determine the age-specific sex ratios of the population.

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ZUSAMMENFASSUNG

In einer vorher veröffentlichten Arbeit (DITUS, 1977a) wurden die Beziehungen zwischen Daten betreffend Verhalten, Ökologie und Demographie einer Population von etwa 450 Hutaffen, *Macaca sinica*, untersucht. Diese Daten weisen darauf hin, dass die Grössen von Trupps (und daher der Population) dem Nahrungsangebot angepasst sind, und durch Ausgleiche zwischen Geburtsraten und Mortalität entstehen. Mortalität wird durch Wettbewerb um Nahrung und weibliche Paarungspartner verursacht. Zugang zu diesen Gütern (oder Rang in der Dominanzhierarchie) und daher die sozial bedingte Mortalität unterscheiden sich je nach Alter, Geschlecht und Verwandtschaft. In dieser Weise bestimmt Sozialverhalten die Alters- und Geschlechtszusammenstellung und die Bevölkerungsdichte der Sozietät und der Population.

Die Evolution dieser Sozialverhaltensweisen wurde in dieser Veröffentlichung besprochen.

Unterschiede im Durchschnittsgrad der Verwandtschaft (r) zwischen Tieren unterschiedlichen Alters und Geschlechtes innerhalb eines Trupps wurden entsprechend ihrer einzelnen Wanderungsraten geschätzt. Erwachsene Weibchen innerhalb eines Trupps sind miteinander und mit allen Säuglingen und Jungtieren verwandt. Die Evolution von Sozialverhalten, welches die Mortalität je nach Alter und Geschlecht unterschiedlich bestimmt, wird im Lichte von klassischer und verwandtschaftsbedingter Auslese besprochen. Unterwerfendes Verhalten wird durch dominante Tiere erzwungen, und wird unter klassischer Auslese allein als anpassungsfähig betrachtet. Der Verlust in Fitness durch eine untergeordnete Tat muss daher nicht durch einen gleichgrossen oder grösseren Gewinn von "inclusive fitness" kompensiert werden um sich in der Evolution zu entwickeln. Unter Verwandten gewinnt der Untergeordnete jedoch zusätzliche "inclusive fitness". Unterwerfendes Verhalten zwischen Verwandten gilt als "erzwungene Selbstlosigkeit" (imposed altruism) oder "erzwungenes Verwandteninvestment". Duldung von Nachkommen oder von untergeordneten Verwandten gelten als Elterninvestment und "willkürliches Verwandteninvestment", in dieser Reihenfolge.

Beziehungen zwischen dominanten und untergeordneten Tieren haben meistens einen Austausch von Futter oder anderen Gütern zur Folge, welche das Überleben und Fitness beeinflussen. Daher wird angenommen, dass der Grad in welchem Individuen unterschiedlichen Alters und Geschlechtes sich gegenseitig drohen oder ausbeuten, dem Grad von Elterninvestment oder Verwandteninvestment zwischen ihnen direkt oder umgekehrt entspricht. Solches Investment ist dem Geschlechtsunterschied der Fortpflanzungsstrategie angepasst, und dient dazu um maximale Fitness der Eltern und Verwandten zu gewinnen. Bevor Männchen die Geschlechtsreife und Fortpflanzungsbereitschaft erreichen, zeigen sie grössere Ansprüche für ihr Wachstum und in ihrer Mortalität, besonders während der Pubertät nachdem sie den Muttertrupp verlassen haben, als weibliche Altersgenossen. Eltern und Verwandte vermeiden diesen möglichen Fitnessverlust durch ihre männlichen Nachkommen, indem sie mehr in Männchen vor dem Auswanderungsalter investieren, auf Kosten weiblicher Jungtiere.

Weibliche Säuglinge und Jungtiere erleiden daher grössere Mortalität als ihre männlichen Altersgenossen. Männchen müssen allerdings vor dem Erreichen der Geschlechtsreife auswandern um Investment auf weitere Kosten anderer Verwandten zu vermeiden. Das gesamte Eltern- und Verwandteninvestment ist jedoch gleich gross für die Gesamtheit aller Männchen, verglichen mit der aller Weibchen, weil das Investment in Weibchen ihr ganzes Leben weitergeht, während es in Männchen aufhört, wenn sie als Adoleszente auswandern. Infolgedessen ist für die männlichen und weiblichen Kohorten (1) Überlebensrate und (2) Verbrauch beworbener Güter gleich gross. Selbstlose und ausbeutungsmässige Verhaltensbeziehungen zwischen Verwandten und nichtverwandten Weibchen und Männchen sind erklärbar als Ausgleich zwischen Verlust und Gewinn in Fitness, welcher aus diesen Verhaltensbeziehungen erwächst.

Im Vergleich zu stabilen Bedingungen ($R_0 = 1$), bewirkt eine Verringerung des Nahrungsangebotes ($R_0 < 1$) eine erhöhte Mortalität unter Säuglingen und jungen Jungtieren, besonders unter weiblichen Jungtieren; während ein reiches Nahrungsangebot ($R_0 > 1$) die Überlebensraten dieser Tiere fördert. Daher, wenn das Vorhandensein beschränkender Güter sich ändert, verändert sich die Wirkung von Eltern- und Verwandteninvestment, und wahrscheinlich dessen Natur selbst, ebenfalls um maximale Fitness unter den neuen ökologischen Bedingungen zu erreichen.

Ich schlage vor, dass die Regelung der Bevölkerungsgrösse und der Geschlechts- und Alterszusammenstellung der Population durch agonistisches und geselliges Sozialverhalten, welches durch klassische und verwandtschaftsbedingte Auslese in der Evolution entwickelt worden ist, entsteht. Das Sozialverhalten (1) bestimmt, unterschiedlich je nach Alter, Geschlecht und Verwandtschaftsgrad (r), Zugang zu lebensnotigen Gütern (und weiblichen Partnern), und daher dementsprechend das Wachstum und die Mortalität von Individuen. Das Sozialverhalten (2) dient dazu, die maximale klassische Fitness von nichtverwandten Tieren und die maximale "inclusive fitness" von verwandten Truppmitgliedern je nach Fortpflanzungsstrategie (Geschlechtsunterschiede in Körpergrösse und Verhalten unter Erwachsenen), und das Vorhandensein von beschränkenden Gütern, zu erlangen. Das Sozialverhalten (3) stellt daher die Sozietät (und Population) auf ein Gleichgewicht mit der vorhandenen Nahrung und der von aussen hervorgerufenen Mortalität ein.

Obwohl Daten von anderen Primaten, welche die Kernfragen dieser Veröffentlichung betreffen, rar sind, stimmen sie im allgemeinen weitgehend mit denen von *M. sinica* überein. Dies lässt vermuten, dass die Hypothesen und Schlüsse, die auf Grundlage der Daten von *M. sinica* dargestellt wurden, auch auf andere Arten, welche eine Sozialorganisation ähnlich der von *M. sinica* haben, anwendbar sind.

Indem Eltern- und Verwandteninvestment sich anpassen, um je nach dem Grad des Geschlechtsdimorphismus maximalen Fitness zu erreichen, dürfte man vermuten, dass Eltern- und Verwandteninvestment und dadurch die Alters- und Geschlechtszusammenstellung der Population, je nach der Grösse des Unterschiedes zwischen männlicher und weiblicher Fortpflanzungsstrategien, sich variieren. Ein monomorphisches Paarungssystem (z.B., *Lemur* und *Hylobates*) würde eines ungefähr gleichen Investments zwischen den Geschlechtern im Nachwuchs bedürfen. Die Geschlechtsquotienten sollten daher auf Gleichheit in allen Altersstufen bestrebt sein. Bei Arten (z.B., *Erythrocebus* und *Papio*) in denen erwachsene Männchen bedeutend grösser als Weibchen sind, sollte das verlangte höhere Investment, um kräftige erwachsene Männchen zu entwickeln, durch eine Verringerung der Zahl von erwachsenen Männchen kompensiert werden. Die Auslese für andere lebensnotige Anpassungen könnte den Einfluss der "intrasexual" Auslese auf den Grad des Geschlechtsunterschiedes beschränken, und in dieser Weise das Investment und dadurch die Bevölkerungszusammenstellung beeinflussen. Fortpflanzungsstrategie (Geschlechtsdimorphismus), andere lebensnotige Anpassungen und das Vorhandensein beschränkender Güter beeinflussen soziales Verhalten, welche weiter die Alters- und Geschlechtszusammenstellung der Population entscheiden.