

The Relation between Ecology and Social Structure in Primates

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Selected data on primate social systems will be discussed and reinterpreted in this article, with a view toward modifying the existing concepts about the adaptive nature of these social systems (1-3). In light of recent data, we limit the concept of the multi-male troop (2) and call attention to the reproductive group as an organic unit that shows stages of growth and decline which may vary under different environmental circumstances. To this end, we introduce a new category of social structure for the primates—the age-graded-male troop. Before proceeding with the definitions and discussions, we must put the data into a historical framework.

The Existence of "Species Typical" Social Organization

The cornerstones of Carpenter's theories of primate social structure (4) can be summarized as follows: (i) primate troops tend to have more or less exclusive home ranges (5); (ii) the average size of a troop tends to be typical for a given species (the term "apoblastosis" defines the process whereby primate troops divide to restore a species-specific balance in numbers); and (iii) the composition of the troop, with

respect to the proportions of sex and age classes, tends to be relatively invariant, regardless of troop size. The ratio of males to females was termed the "socio-economic sex ratio." This ratio tended to be species-specific, and, for most species, there were more adult females than adult males in a given troop. Two corollaries followed: first, there was a strong polygynous trend in most primate species; second, extra adult males were excluded from the troop by some process, to dwell either in a peripheral subgroup of their own or as solitary individuals.

In line with Carpenter's generalizations and some early theories of social evolution, most field workers believed that the behavioral attributes of a species were relatively constant and reflected species-specific adaptations. It was assumed that social structures resulting from the defined patterns of interaction of a given species would manifest themselves as rather predictable entities (1, 2). This assumption still has heuristic value, but the task is much more complex, since, for most primate species, social structure varies with habitat. This has been amply demonstrated for the olive baboon, *Papio anubis* (6, 7), the gray langur, *Presbytis entellus* (8-10), and the vervet monkey, *Cercopithecus aethiops* (11, 12). On the other hand, some species appear to have a standardized form of social organization—for example, the lar gibbon, *Hylobates lar* (13, 14), and the hamadryas baboon, *Papio hamadryas* (15, 16).

The causes of intraspecific variation in social structures are related, in part, to differences in habitat (especially factors of food availability and predation), as well as to differences intrinsic to the troop itself (3); however, once the range in the variation of troop structure is described, a "modal" social organization for a given species can often be discerned, thus facilitating comparisons with other species. It would appear that one generalization is possible: those species that exhibit a wide range of adaptation to differing habitats often show an equally wide range in social structure [for example, *Papio anubis* (6) and *Presbytis entellus* (9)]. On the other hand, species that show a uniform adaptation to specific kinds of habitats often show a corresponding uniformity in their grouping tendencies (1). In fact, when a group of allopatric species shares the same relatively narrow range of adaptation, then this group begins to exhibit a predictable "adaptive syndrome" with respect to feeding, anti-predator behavior, spacing mechanisms, and social structure. Examples from two separate "syndromes" are (i) the arboreal, leaf-eating monkeys of Africa and Asia [*Presbytis cristatus* (17), *Presbytis johni* (18), *Presbytis senex* (19), and *Colobus guereza* (20)] and (ii) the slow-moving, insectivorous loroids of Africa and Asia [*Arctocebus*, *Perodicticus*, *Nycticebus*, and *Loris* (21-23)].

Grades of Social Structure—

A Reassessment

It has not been uncommon to find primate societies classified into grades based on supposed increases in social complexity. The implicit suggestion was that higher grades were achieved through evolutionary stages, but it was well recognized that, within and among each major primate taxon, considerable parallel evolution had occurred (1, 2). Even within the morphologically conservative Prosimii, social organizations equal in complexity to those of the

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Table 1. Range of social organization and feeding ecology for selected primate species (see text for descriptions).

Solitary species	Parental family	Minimal adult ♂ tolerance* (uni-male troop) †	Intermediate ♂ tolerance‡ (age-graded-male troop) †	Highest ♂ tolerance§ (multi-male troop) †
A. Insectivore-fruitivore	A. Fruitivore-insectivore	A. Arboreal folivore	A. Arboreal folivore	A. Arboreal fruitivore
Lemuridae <i>Microcebus murinus</i> <i>Cheirogaleus major</i>	Callithricidae (Hapalidae) <i>Saguinus oedipus</i> <i>Cebuella pygmaeus</i> <i>Callithrix jacchus</i>	Cebidae <i>Alouatta palliata</i>	Colobinae <i>Presbytis cristatus</i> <i>Presbytis entellus</i>	Indridae <i>Propithecus verreauxi</i>
Daubentonidae <i>Daubentonia</i> <i>madagascarensis</i>		Colobinae <i>Colobus guereza</i> <i>Presbytis senex</i> <i>Presbytis johni</i> <i>Presbytis entellus</i>	Cebidae <i>Alouatta palliata</i>	Lemuridae <i>Lemur fulvus</i>
Lorisidae <i>Loris tardigradus</i> <i>Perodicticus potto</i>	Cebidae <i>Callicebus moloch</i> <i>Aotus trivirgatus</i>	B. Arboreal fruitivore	B. Arboreal fruitivore	B. Semiterrestrial fruitivore-omnivore
B. Folivore	B. Folivore-fruitivore	Cebidae <i>Cebus capucinus</i>	Cebidae <i>Ateles geoffroyi</i> <i>Saimiri sciureus</i>	Cercopithecidae <i>Cercopithecus aethiops</i> <i>Macaca fuscata</i> <i>Macaca mulatta</i> <i>Macaca radiata</i> <i>Papio cynocephalus</i> <i>Papio ursinus</i> <i>Papio anubis</i> <i>Macaca sinica</i>
Lemuridae <i>Lepilemur mustelinus</i>	Indridae <i>Indri indri</i>	Cercopithecidae <i>Cercopithecus mitis</i> <i>Cercopithecus campbelli</i> <i>Cercopithecus albigena</i>	Cercopithecidae <i>Miopithecus talapoin</i>	
	Hylotidae <i>Hylotates lar</i> <i>Symphalangus syndactylus</i>	C. Semiterrestrial fruitivore-omnivore	C. Semiterrestrial fruitivore-omnivore	Pongidae <i>Pan satyrus</i>
		C. Semiterrestrial fruitivore	Cercopithecidae <i>Cercopithecus aethiops</i> <i>Cercocebus torquatus</i> <i>Macaca sinica</i>	
		Cercopithecidae <i>Erythrocebus patas</i> <i>Theropithecus gelada</i> <i>Mandrillus leucocephalus</i> <i>Papio hamadryas</i>	D. Terrestrial folivore- fruitivore	
			Pongidae <i>Gorilla gorilla</i>	

* Troop with one adult male and strong intolerance to maturing males. † "Troop" refers to the basic social grouping of adult females and their dependent or semidependent offspring.

‡ Troop with several mature, adult males and age-graded series of males. § Troop typically showing

Cebidae and Cercopithecidae were formed (24, 25).
 The so-called solitary-living species are characterized by a minimum amount of direct social interaction with conspecifics of either sex in the same age class. Typically, the "mother family" (that is, an adult female and her dependent offspring) forms the only cohesive social unit that indulges in daily, intimate interaction. Nevertheless, solitary species, whether primates, carnivores, or rodents, have a social life (26), and indirect communication is maintained among adults that have neighboring or overlapping home ranges. The communication channels of solitary species are characterized by olfactory and auditory modalities which maintain spacing except at mating times (1, 22). The terms "solitary," "asocial," and "dispersed" have been objected to (27) because they obscure the fact that a given pair of adults and their sub-adult descendants can share a home range completely or partially, even though they do not indulge either in communal nesting or regular physical contact. In addition, when there are overlapping home ranges, the same adult pair can reproduce in subsequent years; thus, although individuals are dispersed, a family structure and relatively closed breeding unit (28) are maintained. For example, in *Microcebus murinus* and *Galago demidovii* (29), the home ranges of adult females may overlap considerably. A reproductive male's home range includes the home ranges of from one to six females and their juvenile offspring, while extra males live on the periphery of the dominant male's home range, either as solitary individuals or as a noncohesive bachelor group. The spatial distribution of the adults (29) implies a polygynous breeding system (see Fig. 1). Other nocturnal prosimians appear to exhibit a similar spacing system—for example, *Cheirogaleus major*, *Daubentonia madagascarensis*, *Loris tardigradus*, *Perodicticus potto*, and *Lepilemur mustelinus* (22-24, 30) (see Table 1).
 The parental family structure is characterized in its extreme form by a bonded pair of adults and their immature descendants. This bonded state occurs rarely within the order Primates [assuming the term "bond" includes only social relationships between specific individuals based on the performance of mutually reinforcing activities, in addition to mating behaviors (31)]. It follows then that grooming, huddling, and other nonsexual behavior

engaged in on a daily basis by two individuals of the opposite sex defines the pair bond.

Marmosets of the genera *Saguinus*, *Cebuella*, and *Callithrix* are examples of the bonded parental family (32, 33). These marmosets exhibit a unique form of parental care, in that the male participates to an extent unparalleled by the other families of Primates (1, 32). The male marmoset typically transports the young from the time they are born, transferring them to the female only for nursing (33).

The gibbons, *Hylobates* and *Symphalangus* (13, 14, 34), as well as some species of the family Cebidae [notably the Titi monkey, *Callicebus moloch* (35)], show grouping tendencies similar to those of the marmosets in that a single adult pair and their dependent offspring occupy a given home range, but the male's participation in the care of the young is limited. For example, *Callicebus* and *Aotus* males (36) transport the young to a certain extent and thus appear to be somewhat closer to the marmoset pattern (33), while gibbons and *Indri* males participate little in the rearing of infants. Thus, at least two subvariants of the parental spacing system must be designated: (i) mutual participation by the male and female in the rearing of offspring and (ii) limited or no direct participation by the male in the rearing of dependent young (see Table 1).

Parental groups have probably evolved by at least two different pathways (Fig. 1). The parental group, a more cohesive form of primate social structure, can easily be derived, in a phylogenetic sense, from the more dispersed systems of some of the prosimians, for example, *Galago demidovii* or *Microcebus murinus* (29).

If only adult female primates were to form affiliations, an extended mother family would exist, given that the exclusion of excess adult males takes place through the aggressive action of the parental adult male. If the parental male were closely bonded to the extended group of mothers and daughters, the result would be a typical uni-male group (Fig. 1). Extra-group males would exist on the periphery of the reproductive units. Recent research on terrestrial African primates (the Patas monkey, *Erythrocebus patas*; *Papio hamadryas*; and the Gelada baboon, *Theropithecus gelada*) has indicated the existence of troops composed of several females, their dependent offspring, and one sexually mature, adult male

(16, 37, 38). In such species, troops can also contain a few maturing males as a normal transitional stage in the life cycle of the troop; however, the young males generally leave the parental troops as subadults and join bachelor bands.

The uni-male troop is more complex in its structure than is the parental group because there is an increased representation of sex and age classes in the troop. Adult females must be tolerant of one another and have affiliation mechanisms to promote cohesiveness (39). The behavior of the adult male toward females can also contribute significantly to cohesiveness, since he may "discipline" the females that stray from his group, thereby keeping the group intact [for example, *Papio hamadryas* (16, 40)]. Such herding behavior by the adult male is not typical of all species with a uni-male configuration; it has not been reported for *Cercopithecus campbelli* (41), for example. New uni-male troops can be formed in *Papio*

hamadryas when a solitary younger male is able to "capture" a subadult female from a structured breeding unit. Other variations on this theme are discussed by Kummer (16).

One of the more intriguing aspects observed in some primate societies was that several adult males could and did associate continuously with adult females and young. Because of the contrast with other mammalian taxa that have complex social structures in which males are not permanent members of the group, the "multi-male group" came to be thought of as an advanced and almost unique characteristic of higher primates (1, 2, 4). While some species do have a multi-male troop, it is obvious that the concept has been applied too broadly (42). An intermediate form of social organization, between the uni-male and the multi-male structures, should be recognized. This may be termed the age-graded-male troop. Although several males of varying ages coexist in such troops,

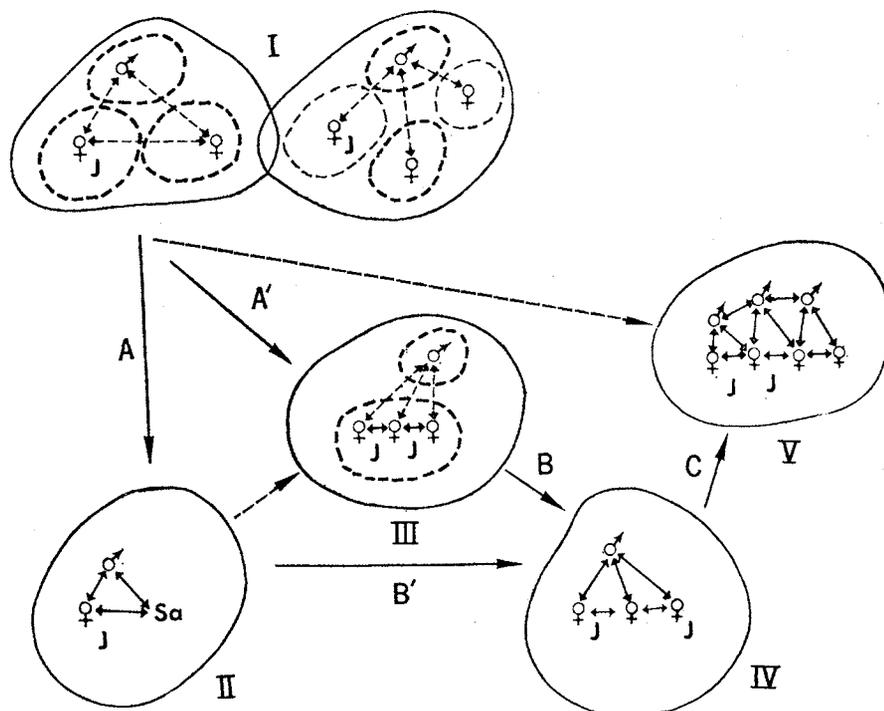


Fig. 1. Space utilization patterns for selected mammals with hypothetical evolutionary pathways. (I) Solitary pattern: adult males and females have separate centers of activity and encounter infrequently. The extended ranges of the males overlap with the home ranges of the females. Only polygynous patterns are presented; *Microcebus murinus* (29). (II) Family group: a bonded pair and their subadult offspring travel as a homogeneous unit in an exclusive home range; *Saguinus oedipus* (32). (III) Uni-male group (extended mother family): an adult male is in periodic contact with a cohesive group of adult females and their progeny; *Ateles geoffroyi* (46). (IV) Uni-male group: an adult male is in relatively constant contact with a cohesive group of adult females and their progeny; *Papio hamadryas* (16). (V) Multi-male group: a cohesive group of several adult males and females with their progeny; *Papio anubis* (49). Hypothetical phylogenetic steps in the formation of mobile, cohesive groupings are indicated by arrows. Routes A, B', and C or A', B, and C are the most probable steps in the formation of cohesive, multi-male groups (1). The arrows formed from dashed lines are less probable evolutionary pathways (1). For simplicity, the symbols J (juveniles) and Sa (subadult) have been included only occasionally to indicate the presence of immature animals.

there are proportionately fewer males in these troops than there are in true multi-male troops (whose sex ratio may approach 1:1) (6). The linear male dominance order is based on the age of the males, with no definable subunit of several males in the oldest age bracket. The lack or absence of fully adult males of equivalent age is the characteristic that defines an age-graded-male troop [for example, troops of *Mandrillus leucocephalus*, *Presbytis entellus*, and *Ateles geoffroyi* (43-47) (see Table 1)].

The age-graded-male troop may be considered a phylogenetic step toward the true multi-male configuration (see Fig. 1), with the former having an intermediate level of male tolerance that allows several young males to mature longer within the troop of their birth than do young males in uni-male troops. Nevertheless, a fundamental tendency toward polygyny and the possibility of the troop's splitting and returning to a uni-male condition remain. Thus, the age-graded-male troop is a variation on the uni-male theme (see Fig. 2). What appears to distinguish species with an age-graded-male troop from species with a strong uni-male tendency is (i) the adult "leader" male exhibits a wider range of tolerance of young males near his own age and (ii) part of the tolerance shown by the dominant male appears to derive from the fact that

these species generally have larger troops. In addition, the larger troops have larger home ranges and therefore more possibilities for dispersing into subgroups while foraging. This very tendency toward fractionation can generate new troops by apoblastosis (4).

Members of the genus *Papio*, particularly the species *ursinus*, *anubis*, and *cynocephalus*, are adapted to savannas and forage a great deal on the ground, although they retire to rocky places or trees for sleeping at night (48, 49). These species exhibit classic multi-male groups [as do, with some limitations, the semiterrestrial macaques, including *Macaca mulatta*, *M. fuscata*, and *M. speciosa* (50-52)]; however, to classify other primate species that have more than one male in the troop as multi-male and then to rank these species within the same grade of social structure as these terrestrial macaques and baboons is to oversimplify matters.

The multi-male troop is characterized by an oligarchy of adult males that are roughly equivalent in age (49). These males show affiliation behaviors, and, although they may be ranked in a dominance order, the ranking is not pronounced within the oligarchic subgroup. Cooperation exists among the superdominant males (39), and they actively oppose and dominate younger males in the subadult age class (49). Species exhibiting a multi-male config-

uration do, of course, have within them males that may be arranged in an age-graded series (53, 54). Furthermore, there may be solitary males that live independently of the troops and that join and leave troops in a semiregular pattern (55, 56).

The multi-male troop was first defined for *Papio anubis*, primarily in the pioneer studies of Washburn and DeVore (48, 49). Baboons were portrayed as living in cohesive troops of 30 to 50 animals; solitary males were not described originally (48), but were subsequently noted for *Papio cynocephalus* (56). The multi-male troop appeared to serve as an antipredator device, since the presence of many adult and subadult males permitted collective attack should the troop be menaced by a terrestrial predator.

Although the sex ratio at birth is almost equal in *Papio* and *Macaca*, the number of reproducing females for each adult male varies from one to three. Any difference in the adult sex ratio is presumed to result from both differential mortality and the differential maturation rates of the sexes. The adult males are organized in a dominance hierarchy, and the alpha male does most of the breeding during the peak of a female's estrous period (49, 54).

Recent studies by Rowell (6) and Altmann and Altmann (56) indicate that in both forest and savanna habitats baboons of the genus *Papio* show neither such strong dimorphism in social roles nor such a disparity in the male-female sex ratio as was originally described (57). In light of more recent evidence, we will probably have to alter our concept of the baboon social life. Nevertheless, the existence of several adult males of an equivalent age serves to crystallize and define the concept of the multi-male troop.

In previous reviews of primate social organizations, the uni-male groupings characteristic of *Erythrocebus patas* (37), *Papio hamadryas*, and *Theropithecus gelada* (16, 38), all three of which are adapted to arid climates, were considered specialized offshoots of the multi-male grouping that supposedly characterized most advanced primates (2, 3). This tendency to characterize most primate species by a multi-male social structure and to set aside those species exhibiting uni-male groups as cases of adaptation to extreme environments was motivated, in part, by a desire to emphasize the uniqueness of

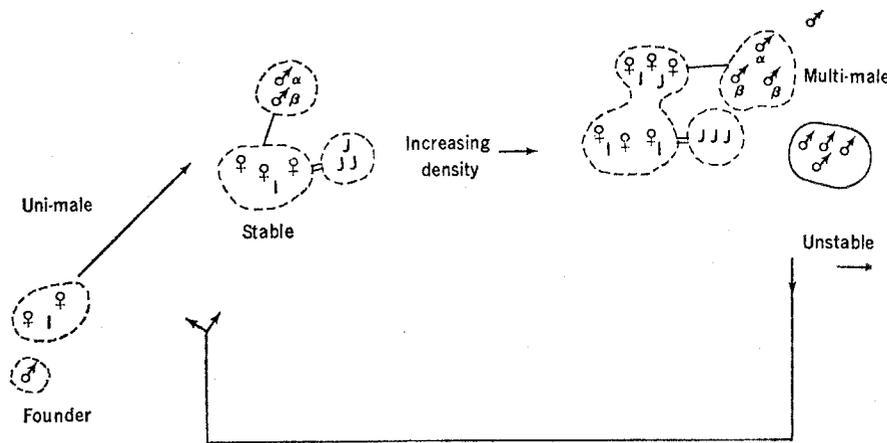


Fig. 2. Hypothetical diagram of troop growth for arboreal primates. The assumption is that a uni-male tendency is the most typical configuration at moderate population densities. Given a founder situation at the left, consider an adult male attached to a cohesive unit of two adult females and their young. The troop grows by recruitment, yielding a subgroup of juveniles and a beta male that is subdominant to the alpha male or father. The two older males form a subgroup in their own right. At greater densities, younger males may form a peripheral subgroup of their own that has no direct contact with the basic subgroup of mothers and their young. The subgroup of adult males may now be augmented slightly to three, with the founding father still dominant. Although the troop now appears to be multi-male, it would be more correct to consider it an age-graded-male group. Splitting of the new unstable troop can lead to the original uni-male configuration (19, 47, 66).

primate societies when contrasted with the social groupings of other mammals.

The preoccupation with the concept of the multi-male organization was unfortunate for at least two reasons: (i) male-male tolerance mechanisms were studied to the virtual exclusion of the equally complex spacing and affiliation mechanisms exhibited by females [as an example of such exclusive attention see (58)], and (ii) differences in the roles of males among the various species exhibiting so-called multi-male systems were masked by lumping a broad range of species-typical social organizations under the term "multi-male groups." In support of this last statement, it should be pointed out that the multi-male troops of the lemurid primates, such as *Lemur catta* and *Propithecus verreauxi* (25, 59), are organized around a female matriarchy that differs markedly in discrete social control mechanisms from the multi-male troops of the savanna baboons, *Papio anubis*, *P. ursinus*, and *P. cynocephalus* (56, 57).

The preoccupation with the "unique," the desire to relate primate behavior to human behavior, and the lack of sound ecological studies are hindrances at this stage of our understanding. What is needed more than ever is a clear appraisal of primate species as mammals exploiting an ecosystem and subject to ecological pressures similar to those acting on other mammalian species (3).

We propose that not only terrestrial primate species adapted to arid climates but also most primate species adapted to forests are characterized by either uni-male troops or age-graded-male troops. The true multi-male system is a less frequently evolved specialization, and the term "multi-male" should be restricted to those species having large troops that include several functionally reproductive adult males, as well as nonreproductive males of different ages.

Regulation of Troop Size

One of the key problems in describing a multi-male troop involves the definition of an adult male. In censusing primate troops, most workers use the category "adult male" for males that are sexually mature; however, it is well known that the age of sustained spermatogenesis does not necessarily correlate with the age of "social" maturity. In most medium-sized primates, a male

Table 2. Comparison of the populations of *Presbytis senex* found at Polonnaruwa and Horton Plains (19). (Population densities are minimum estimates that may show higher levels in more restricted sample areas.)

<i>Presbytis senex</i>	Polonnaruwa	Horton Plains
Number of troops studied	33.0	27.0
Total population studied	278.0	229.0
Population density (per square kilometer)	215	92.6
Percent of adults in population	63.8	51.3
Percent of subadults and juveniles in population	14.1	30.7
Percent of adult males in adult population	28.2	36.7
Percent of adult females in adult population	71.8	63.3
Ratios of adult males to adult females in total population	1 : 2.5	1 : 1.7
Average number of animals in uni-male troops	8.4	8.9
Average number of animals in predominantly male troops	7.5	7.5
Ratio of adult males to adult females in uni-male troops	1 : 4.1	1 : 3.3
Number of infant deaths*	19.0	2.0

* Based on one complete reproductive period.

that has become sexually mature at 3 to 5 years of age may not be sociologically mature or physically dominant until 8 or 9 years of age—yet all of these males are lumped together as adults. A similar social maturation sequence has been described in elephants, for which the problems of age-class definition are comparable to those encountered in primates (60, 61).

Long-term studies of *Macaca fuscata* and *M. mulatta* show how roles are established and maintained and how males succeed to leadership (54, 62–64). The rank of young males in later life is, in part, dependent on the status of their mothers (63). Fractionation of a large troop to form two new troops may be accompanied by the deposition of an old leader, the assumption of leadership by a solitary male, or the succession to leadership of second- or third-ranking males upon the removal or loss of an old leader (62, 64). Without recounting the extensive research on this, we wish to make the point that the processes of splitting do not necessarily involve extensive mortality in the infant and juvenile age classes. Furthermore, the new troops thus generated are not essentially uni-male in structure.

Figure 2 shows the hypothetical growth of a primate troop from a founder situation to eventual instability and breakup because of internal recruitment and crowding that resulted from close neighbors. More data are needed on the natural genesis of troops, since we believe that there is a strong tendency toward a polygynous, uni-male reproductive unit for most species of forest-dwelling primates in the New World and Old World (65).

The case of a Mona monkey, *Cerco-*

pithecus campbelli lowei (66), troop parallels the diagram in Fig. 2. From 1964 to 1968, the troop increased in size because of births to the founder adult male and four adult females. In the years 1968 to 1970, the number of births was curtailed and four young adult males from 3 to 4 years of age emigrated. During this transition period, the tendency toward a uni-male structure was masked and the troop might have been called multi-male.

Ateles geoffroyi and *A. belzebuth* maintain an age-graded-male troop (46, 47, 67). In contrast to *Cercopithecus campbelli lowei*, adult male spider monkeys are not in continuous association with adult females and young. Instead, an *Ateles* "group" is composed of units that contain one or more females and their dependent young and that forage independently in a common home range. The adult male will accompany the female units when females are in estrus and when there exist special positive, dyadic relationships between individuals. The age structure of the males, based on birth intervals, lends itself to the formation of an alpha-beta-gamma dominance hierarchy. Among subadult males, mutual support may be shown during offensive and defensive behavior toward potential predators and intruders, but with increasing age some young males become peripheral.

The range of social organization encountered in *Ateles geoffroyi* in either space or time is given in Fig. 2. At one extreme is the founder situation, or so-called uni-male group. The social organization of this species is generally several females and a semidetached male group that is, in essence, an age-

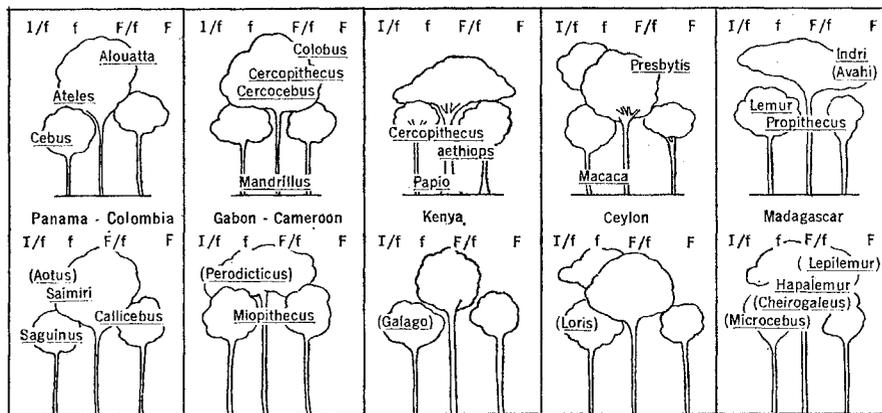


Fig. 3. Ecological equivalence for selected primate species. Horizontal scaling: I/f, insectivore-frugivore; f, frugivore; F/f, folivore-frugivore; F, folivore. Since the feeding categories are not absolute, only relative trophic preferences are indicated. The midpoint of the name should lie at the modal feeding classification. Vertical scaling: relative feeding height is illustrated by the position of the name. Lowest position: semiterrestrial; middle position: arboreal, second growth; highest position: upper canopy feeder. Names in parentheses indicate a rhythm of nocturnal activity. The upper series are all medium to large primates (adult weight, greater than 5 kilograms); the lower series are all small primates generally (adult weight, less than 2 kilograms).

graded group, since there is a male hierarchy based on age and most of the mating during a peak of a given female's estrus is probably accomplished by the older, dominant male. With denser populations, there are larger groups of females and more peripheral males, and there may be fighting among males when associated with female groups (68).

The genesis of two new troops from a single large troop in those species exhibiting the age-graded-male system can occur without a take-over of leadership or fighting among males. For example, division of a large *Presbytis entellus* troop consisting of approximately 30 individuals would begin by a departure from the sleeping tree and a fractionation into two foraging subgroups, each subgroup being under the leadership of a different male. The largest subgroup of females would follow the dominant male, the second subgroup following a subdominant male. At the conclusion of the day's foraging, the animals would return to a common sleeping place. The females themselves would exert a powerful influence on the ultimate composition of the subgroups, depending upon which male they followed. The second stage in troop development would consist of separate foraging patterns and occasional utilization of different sleeping trees. Eventually, the subgroups would be foraging and sleeping independently; thus, two new troops would be created. Examples are further amplified for *Presbytis entellus* by Muckenhirn (44).

Long-term population studies on Barro Colorado Island permit some generalizations concerning the grouping tendencies of *Alouatta palliata*, the howler monkey (69, 70). Chivers (71) has summarized the data for the island population and for one troop (the laboratory group) in particular. Although this species is often cited as exhibiting a multi-male structure, peripheral or extra-group males exist and uni-male troops occur frequently. It would appear that, at low population densities, this species approximates a uni-male structure (72), while at higher densities a temporary age-graded-male structure appears. We must reemphasize that, when there exists an age-graded series of related maturing males with one older, dominant male, then the multi-male structure is more apparent than real. In fact, in large troops of *Alouatta palliata* with several mature, adult males, there appears to be curtailed reproduction (73). This, then, leads us to consider some of the ecological factors that lead to the division of troops and what forms of social pathology may result in high-density populations.

Social Pathology and Density

For many primate species, the conditions under which splitting and male "take-overs" can occur are, in part, related to the density of, and degree of disturbance in, the population (19). Alternatively, fractionation of large groups

can occur under ecological conditions (such as dispersed resources) that favor the maintenance of small groups and that may even approximate the founder situation (12).

Presbytis senex of Ceylon shows some rather instructive trends in population growth and composition when high-density populations are compared with low-density populations. As Table 2 indicates, *Presbytis senex* tends to live in uni-male reproductive units (19, 74) and is found in a wide range of habitat types, from a lowland dry zone (Polonnaruwa) to a highland wet zone (Horton Plains). Extra-troop males are organized into groups having an average size of 7.5 individuals. In high-density populations, the uni-male reproductive groups are subject to harassment from the peripheral bachelor groups, which occasionally results in infant mortality and leadership take-overs. Infant mortality is reflected, in part, by the different percentages of subadults and juveniles in low- and high-density populations (see Table 2). In Sugiyama and Mohnot's studies in India, *Presbytis entellus* infants were actually attacked and killed by invading adult males (10, 45). In the Ceylon langurs, Rudran did not witness such events directly, but infants and juveniles were found to be injured or missing after a male replacement had occurred. This type of male replacement appears to occur under conditions of high population density (9) or in marginal habitats (45); in either case, the altered age structure that results from male take-overs curtails population growth to some extent.

The suggestion that the uni-male structure is a response to crowding stress has been made before (12). The tendency for captive primate groups to assume a uni-male or "despot" male configuration was often assumed to be a pathological response; however, we believe that, although this uni-male condition may manifest itself at crowding densities, it is erroneous to think of the uni-male structure as being pathological.

Some Correlations between Social Structure and Ecology

The history of primate evolution has been subject to many reviews (75). Beginning with an insectivore-like form exhibiting certain arboreal adaptations with rather enlarged eyes, the primates

underwent an extensive radiation throughout the Paleocene, giving rise to two main branches. One major branch differentiated into the present-day galagos, lorises, and lemurs, while the other differentiated into the Old World monkeys, New World monkeys, tarsiers, pongids, and hominids. The lorises and galagos still persist in Africa and South Asia as nocturnal, forest-adapted forms. These may be considered the most morphologically conservative primates, representing most nearly Paleocene forms.

The island of Madagascar served as a reservoir for the lemuroid primates, and this isolated radiation resulted in the occupancy of feeding niches that replicate, in part, continental niches (76). Deriving from the second major radiation, the neotropical monkeys (Hapalidae and Cebidae) began their adaptations in the Oligocene in isolation from the Old World monkey radiation. Thus, the Madagascan, neotropical, and Palaeotropical radiations can be compared to elucidate convergences.

Judging from the habits of the living primates and the structure of fossil forms, the early primates were nocturnal and arboreal and subsisted on an omnivorous diet, including fruits, small invertebrates, and perhaps small vertebrates. The early radiation took place in a tropical forest habitat, and, in general, present-day primates remain tropical in their distribution, with the greatest diversity of species occurring in the rain forests of West Africa, Indo-Malaysia, South America, and Madagascar. The tropical rain forest, then, is the habitat in which the most complex problems of primate evolution are to be found. Those primate species that have extended their ranges into seasonally arid areas characterized by thorn scrub or savanna are often confined to areas surrounding riverine forests.

The forests were retained by primates as their primary environment. The acquisition of terrestrial habits is recent in primate history and occurred in some species of the now extinct giant lemurs, Arceolemurinae (77), from Madagascar, as well as in the cercopithecine genera *Papio*, *Mandrillus*, *Erythrocebus*, *Theropithecus*, *Macaca*, and *Cercocebus* in the Old World tropics. Terrestrial adaptation within the Pongidae are exemplified by *Pan* and *Gorilla*. Only in South America has a truly terrestrial form not evolved.

Figure 3 compares four geographic

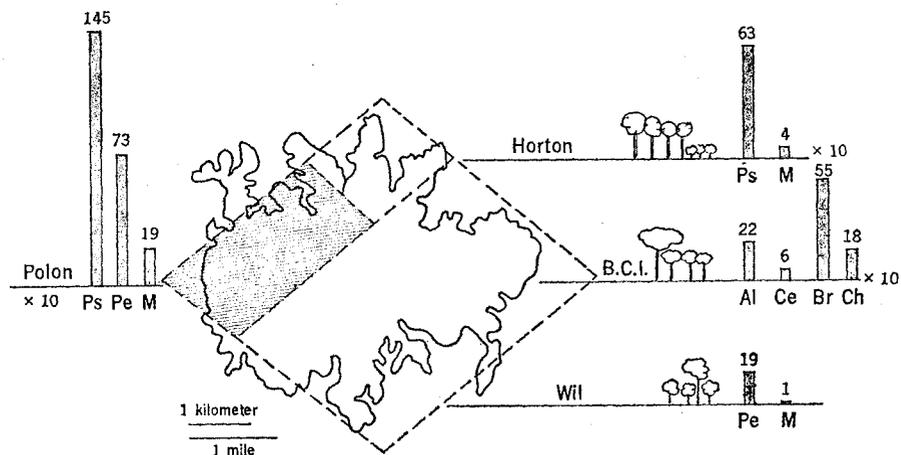


Fig. 4. Primate biomass comparisons for Ceylon and Panama. To compare the sizes of survey areas, the Ceylon study areas are superimposed on an outline map of Barro Colorado Island (B.C.I.). The dashed perimeter outlines the extent of the Wilpattu (Wil) survey area; for comparison, the Horton Plains (Horton) and Polonnaruwa (Polon) study areas are superimposed, and the latter is indicated by shading. To aid scaling on a single diagram, the biomasses for Polonnaruwa, Horton, and B.C.I. are displayed at 1/10 the actual values in kilograms per square kilometer. (Ps, *Presbytis senex*; Pe, *Presbytis entellus*; M, *Macaca sinica*; Al, *Alouatta palliata*; Ce, *Cebus capucinus*; Br, *Bradypus infuscatus*; Ch, *Choloepus hoffmani*.)

areas with respect to the kinds of niches occupied by their respective primate genera. We have classified the genera by activity cycle, height of feeding, diet, and relative size. Many species weighing less than 2 kilograms are nocturnal and show a pronounced tendency to feed on high-energy food resources such as insects and fruit. All small primates are arboreal, and, with the exception of the neotropical forms and the West African *Miopithecus*, are derived from the morphologically conservative loriseid or lemuroid stocks. The larger primate species are almost all diurnal, with the exception of the Madagascan genus *Avahi*. Only among the larger primate species do we find several genera exhibiting semiterrestrial adaptations; these genera include *Mandrillus*, *Papio*, *Pan*, *Gorilla*, and *Macaca*.

The large diurnal primates (the Lemuridae, Indriidae, Cebidae, and Cercopithecidae) display parallel evolution with respect to their feeding strategies; there have been trends away from dependency on energy-rich invertebrates and fruit toward the more readily available cellulose found in leaves. Gut modifications associated with the change in diet can include a larger caecum, as in *Alouatta*, *Indri*, *Avahi* (78), and *Lepilemur* (79), or a chambered stomach and bacterial symbionts, as in *Colobus* and *Presbytis* (80). The latter modifications are convergent with the physiological and morphological adaptations evolved by terrestrial ungulates. Those primate species that can

utilize cellulose in leaves are referred to as folivores and are distinguished from frugivores, which cannot utilize cellulose (81). Of course, these basic categories do intergrade, since folivores may supplement their leaf diet with fruit. Conversely, frugivorous species may utilize leaves for the simple sugar in their parenchyma cells (81).

Not surprisingly, the arboreal folivores are the most numerous of the larger forest mammals, sometimes accounting for 30 to 40 percent of the arboreal mammalian biomass (see Figs. 4 and 5, Tables 3 and 4). Only in the Neotropics does the primate biomass rank second to that of another arboreal mammalian order—the edentate grazer of the treetops, represented by the three-toed sloth *Bradypus* (82) (see Fig. 4).

Social Structure of Arboreal Primates

The smaller, nocturnal, insectivorous prosimians of Asia, Africa, and Madagascar seem to exhibit the same form of social organization. They are solitary or organized into dispersed family groups (22–24). In part, their solitary habits may result from their being nocturnal, since the coordination of groups would be difficult. The solitary state may also correlate with their insectivorous habits, since foraging patterns may demand a solitary technique (22). *Lepilemur* is a folivore, however, and retains the solitary pattern, which sug-

gests that the rhythm of nocturnal activity restricts group formation and coordination. The neotropical night monkey *Aotus* is derived from a diurnal form, and nocturnality is a secondary adaptation. *Aotus* exhibits a parental family structure and is thus partly an exception to the rule established for the prosimians. This may indicate the retention of a phylogenetically old parental system that is still compatible with the rhythm of nocturnal activity (36).

The small diurnal primates concentrated in the New World (*Callicebus*, *Saguinus*, *Callithrix*, and *Saimiri*) are insectivore-frugivores and exhibit two grouping tendencies. *Callicebus*, *Saguinus*, and *Callithrix* live in parental families, while *Saimiri* lives in age-graded-male troops. The parental structure of *Callicebus* and *Saguinus* may be the retention of a phylogenetically conservative trait.

The only small diurnal primate of the Old World is *Miopithecus talapoin*. It shows strong convergences in social behavior and ecology with *Saimiri sciureus* of the Neotropics (83, 84). Both species live in large troops (20 to 100 individuals) that divide into subgroups based on age and reproductive classes (83–85). Although these species are superficially multi-male, adult males show little affiliation with each other or with females except during the breeding season, and young males may form a peripheral group. Furthermore, the form of the social structure is influenced by the breeding season, which leads to dominance among males and the formation of temporary uni-male breeding units (86); hence, the classic multi-male structure is not matched. Table 1 indicates our interpretation of the form of social structure for the smaller species of primates and the correlations with their feeding habits.

Given the two broadly defined feeding niches, folivores and frugivores, the



Fig. 5. Adult male *Presbytis senex*. Dense populations of this arboreal folivore are found in its habitat on Ceylon. In forested areas with sufficient rainfall, this species may account for the greatest primate biomass.

following generalizations can be made about the larger arboreal primates: (i) given comparable habitats, the frugivores have larger home ranges and move more widely during their daily activities than do folivores of an equivalent size class [for example, compare *Ateles* with *Alouatta* (87), and *Presbytis senex* with *Macaca sinica* (88)] (see Table 3); (ii) both trophic types tend toward either a uni-male structure or an age-graded-male system (see Table 1), with folivores especially tending toward a uni-male organization; and (iii) many folivores [*Colobus*, *Alouatta*, and *Presbytis* (19, 20, 71)], but only some of the frugivores [*Symphalangus* and *Hylobates* (14, 34)], employ troop or individual vocalizations in maintaining spacing between adjacent troops.

Comparisons among the African, Asian, and South American forest-dwelling species show the marked tendencies toward a uni-male reproductive unit (see Table 1). In an extensive sur-

vey, Struhsaker lists almost all species of West African rain forest frugivores of the genus *Cercopithecus* as typically exhibiting a uni-male reproductive unit (65). *Cercopithecus mitis*, a frugivore studied in Uganda (89), and *Colobus guereza*, a folivore (20), show similar modes. Examples of uni-male reproductive units found among the strongly arboreal folivores of Asia include *Presbytis cristatus*, *P. johni*, and *P. senex* (17–19). Although some troops of *P. cristatus* may, under certain circumstances, contain more than one male (90), this reflects an age-graded-male system. In Central America, the folivore *Alouatta* may exhibit a uni-male system under conditions of low population density, but at high densities several males may be included in an age-graded-male troop. The frugivorous, white-throated capuchin, *Cebus capucinus*, appears to exhibit a uni-male reproductive system (91), while *Ateles geoffroyi* tends toward an age-graded-male system (92).

The arboreal folivores may be characterized by their vocalizations, which usually take the form of dawn choruses. These announcement calls may also be produced at various times during the day, since they appear to occur prior to progressions and are also triggered by exogenous factors. The role of these calls is definitely related to intraspecific spacing. This function has been demonstrated for *Colobus* (20) and *Alouatta* (71) and is undoubtedly being served by the calling of *Presbytis* (19). The frugivorous gibbons and the siamang exhibit comparable chorusing behavior (14, 93). No investigator has specifically attempted to correlate possible seasonal increases in the frequency of chorusing behavior with breeding peaks for any of the chorusing species. McClure, however, offers observations on *Symphalangus syndactylus* and *Hylobates lar* in Malaysia that suggest such a correlation may exist (94).

Table 3. Some comparisons of home range and group sizes. [Average home range and group size will vary widely from one study area to another. We present only species groups from the same areas for the best relative comparison. (B.C.I. indicates Barro Colorado Island.)]

Species	Locality	Average home range (km ²)	Group size (average)	Feeding class
<i>Alouatta villosa</i> (71)	B.C.I., Panama	< 0.08	14.6	Folivore-frugivore
<i>Ateles geoffroyi</i> (46, 87)	B.C.I., Panama	0.60	12.0	Frugivore
<i>Cebus capucinus</i> (91)	B.C.I., Panama	0.85	15.0	Frugivore
<i>Presbytis senex</i> (19, 74)	Ceylon, Polonnaruwa	0.06	8.4	Folivore
<i>Presbytis entellus</i> (88, 96)	Ceylon, Polonnaruwa	0.14	~ 20.0	Folivore
<i>Macaca sinica</i> (53)	Ceylon, Polonnaruwa	0.15	24.1	Frugivore
<i>Presbytis entellus</i> (44)	Ceylon, Wilpattu	> 1.00	~ 20.0	Folivore
<i>Macaca sinica</i> (53)	Ceylon, Wilpattu	> 1.00	20.0	Frugivore

Social Structure of Semiterrestrial Primates

In general, semiterrestrial species tend to live in variable habitats and are frugivores or varied feeders. *Presbytis entellus* and *Gorilla gorilla* are the only folivorous primates that do forage extensively on the ground. Semiterrestrial species also tend to live in larger groups, compared to arboreal forms of a similar body size, and tend to form age-graded-male troops (see Tables 1 and 3).

All but one species of *Presbytis* and of *Cercopithecus* fit into the two forest niches (arboreal folivore and frugivore) described above. The exceptions are *Presbytis entellus*, which is terrestrially adapted and occupies riverine forests, seasonally dry forests, and seasonally arid scrub (8), and *Cercopithecus aethiops*, which occupies gallery forests and savanna areas (11). Both species show a variable troop structure, with *Cercopithecus aethiops* tending to exhibit an age-graded-male to multi-male configuration (11, 12), and *Presbytis entellus* showing an age-graded-male organization in Ceylon and in some parts of India. *Presbytis entellus*, however, may also show a strictly uni-male pattern when crowded into remnant patches of roadside forest in India (8, 10, 44, 45, 95, 96).

The tendency toward a larger group size and an increased number of males in a group is well illustrated in the forest-adapted mangabeys (*Cercocebus*) when a species that forages on the ground (*C. torquatus*) is compared to a conspecific of similar size that is primarily arboreal (*C. albigena*). The more terrestrial *C. torquatus* forms larger troops with more than one adult male per troop. The sympatric species *C. albigena* forms smaller troops and characteristically has a uni-male group structure (97); however, Chalmers (98) presents data that suggest a multi-male group for *C. albigena* in Uganda.

The tendency toward larger group sizes than those of strictly arboreal forms and an accompanying age-graded-male structure may also hold for semiterrestrial macaques and *Mandrillus*. *Macaca sinica* troops, for example, have a distinct age gradation in the so-called adult male class, as well as extra-group males (53). Recent research by Gartlan (43) suggests that the drill (*Mandrillus leucophaeus*), which forages on the ground in dense forests, has retained the uni-male to age-graded-male structure.

Papio anubis, *P. cynocephalus*, *P. ursinus*, *Macaca mulatta*, and *M. fuscata* forage primarily on the ground (7, 50, 56). They exhibit a multi-male grouping pattern, which seems to be effective as an antipredator mechanism (7, 49) (see Table 1).

Terrestrial species of the genera *Theropithecus* and *Erythrocebus*, as well as *Papio hamadryas*, present other problems. *Theropithecus gelada* and *Papio hamadryas* are adapted to extremely arid environments and break up into foraging parties that are uni-male in composition; hence, the selective advantage of group attacks on terrestrial predators is lost. Crook and Gartlan (2, 3) have suggested that this pattern promotes feeding efficiency by reducing the competition for food that would occur if a large number of males accompanied the females and young; hence, these species have approximated a uni-male grouping at the expense of group offensive behavior toward terrestrial predators. Such foraging units reassemble at selected sleeping sites in the evening.

The mode of antipredator behavior is extremely important to a full understanding of the selective advantage of either a multi-male or uni-male group. The terrestrial *Erythrocebus patas*, for

example, lives sympatrically with *Papio* but has retained the uni-male grouping tendency, with the male keeping watch while the females forage. *Erythrocebus* relies mainly on speed, distraction displays by the adult male, and dispersed hiding to avoid predation; thus, its antipredator behavior is not and never was built around a mobbing response (37). Since *Erythrocebus* is derived from a *Cercopithecus*-like form, it may have retained the uni-male structure in its new habitat and have undergone selection for greater speed instead of evolving a multi-male structure, as is the case in some species of the genus *Papio* (65).

The chimpanzee (*Pan troglodytes*) occupies a range of habitats, from rain forest to forest-grassland. Troops seem to have a loose grouping pattern (99), although cohesive troop behavior may be shown during long marches in savanna areas (100). These frugivores break up into foraging units in which strong cohesion exists mainly in the immediate mother family, although patterns of long-term affiliation are displayed when the independently foraging subunits come together (99, 101).

Gorilla gorilla may be considered a semiterrestrial folivore that has a cohesive group structure. The males appear to be age-graded, with one old, silver-back male as the leader (102).

Table 4. Comparisons of arboreal biomasses. [Data for Ghana from Collins (108); data for Barro Colorado Island are preliminary estimates and represent the minimum; data for Ceylon are minimum estimates that may show higher levels in restricted sample areas.]

Species	Biomass (kg/km ²)	Estimated arboreal biomass* (%)
Barro Colorado Island		
<i>Alouatta villosa</i>	220.0	22
<i>Cebus capucinus</i>	60.0	6
<i>Bradypus infuscata</i>	550.0	54
<i>Choloepus hoffmani</i>	180.0	18
Ghana		
<i>Colobus</i> (three species)	55.08	79
<i>Cercopithecus</i> (two species)	5.3	8
<i>Cercocebus</i> (one species)	2.6	4
Polonnaruwa, Ceylon		
<i>Presbytis senex</i>	1450.0	61
<i>Presbytis entellus</i>	730.0	31
<i>Macaca sinica</i>	190.0	8
Wilpattu, Ceylon		
<i>Presbytis entellus</i>	19.0	< 95
<i>Macaca sinica</i>	< 1.0	> 5
Horton Plains, Ceylon		
<i>Presbytis senex</i>	630.0	94
<i>Macaca sinica</i>	< 40.0	6

* Percentage is based on the known mammalian biomass totals but not the total arboreal mammalian biomass, which may be one-sixth again as high.

Roles, Group Functions, and Social Structure—Some Selective Advantages

Crook (3) has evaluated the interrelations between ecology and social structure in primates. We offer here some comments on critical issues that deserve further research. The fundamental questions are (i) Why do some primate species exhibit a multi-male troop composition? and (ii) Why do adult female primates find it advantageous to form extended mother families? In an evolutionary sense, the number of males in a given troop will depend on what advantage the males are to the reproducing females (103).

It would appear, in comparing the various species of higher primates, that there is a strong trend toward polygyny. Certainly a given male increases his individual fitness by distributing his genes among the greatest possible number of females. However, many advantages can accrue to a dominant male through the presence and actions of subordinates (16, 39). A given male's dependence on other males for support

in enhancing his survival value will determine, in part, the short-term advantage of having many males in a troop. Nevertheless, if fewer males can do the same task better than many males, then all things will tend to favor a polygynous mating system. Even in a multi-male troop, such as has been reported for various species of *Papio* and *Macaca*, it may well be that the descendants of the alpha male would be more predominant within the breeding unit than would those of subordinate males, since subordinate males engage in less sexual activity than do alpha males (49, 54).

In most species of primates, the role of the male involves little parental care. There are, however, exceptions within the families Cebidae and Hapalidae, as well as in some species of the genus *Macaca*. The functions of the adult male, either alone or in company with other males, seem to be (i) to maintain spacing with respect to neighboring troops of the same species, (ii) to reduce competition within the group by driving out younger males, and (iii) to enforce some degree of protection against predators. These behaviors may involve vigilance, mobbing, pursuit-invitation displays, or outright attack.

A fourth aspect of the adult male's activities, which has received only sporadic attention, is his role of providing leadership. By initiating and maintaining movement in a certain direction, the male is influential in promoting cohesion of the troop and serves as a focus for the troop's movements (44, 102). The dominant adult male is the one most likely to initiate a following response from the females, hence his leadership role is dependent upon the active participation of females and attendant juveniles in his movements (44).

In contrast to the roles of adult males, the roles of adult females are dominated by infant care. During the early phases of the infant's development, the mother is responsible for protecting it; when the infant enters the juvenile stages, the mother serves as a focus for its socialization. Indeed, the juvenile's status is, in part, predetermined by its mother's status within the female hierarchy (63).

To some extent, each female old enough to reproduce is in competition with males and other females of the same age class for food, sleeping space, and so on. Nevertheless, certain advantages (for example, increased feeding efficiency and antipredator be-

havior) may be inherent in a group of several females traveling together and maintaining a close liaison. The extent to which individual females benefit from group rearing of their progeny and the extent to which their own chances of survival are increased by associating with other females will determine the size to which the troop can profitably increase.

Ultimately, the size of the troop is, in part, a compromise between competition among members for resources that are in short supply and the advantage of having many members in locating resources that are scattered and available for restricted periods (96). The advantage of feeding in a group is often overlooked by field workers, although feeding calls, which promote aggregation in fruit trees, are a well-known phenomenon for some species.

We speculate that, although primary folivores such as *Colobus guereza* and *Presbytis senex* eat considerable quantities of fruits, their feeding strategy is not predicated on a daily need of finding ripening fruit trees within their home range. Small, cohesive, uni-male social units are permitted within this strategy. However, in frugivores such as *Ateles geoffroyi* and *Pan satyrus* (46, 101), the best feeding strategy involves breaking up the troop into small, independently foraging units that spread out to locate fruit trees within their home range and then "announce" the location of feeding spots. In *Saimiri*, foraging for small, dispersed canopy insects leads to the formation of subgroups that forage at different rates (84). The interaction between the distribution of primary resources (food and water) in a specific habitat and the population density in that habitat can profoundly affect social structure (12).

In rain forests, sympatric species often form mixed feeding groups that move together and show very little overt competition. The phenomenon has been described for Central America and for Gabon, West Africa (104). Such species associations should be distinguished from instances in which an occasional male of one species may associate with a troop of another species [for example, a *Saimiri* male in a *Callicebus* group (35) and two *Macaca sinica* males in a *Presbytis entellus* group (44, 95)]. The exact significance of either the casual or the frequent mixed-species group has not been ascertained, although in both types predator avoidance or feeding effici-

ency, or both, may be increased for all members. The whole problem requires attention (105).

We have referred to antipredator behavior throughout our consideration of selective advantages for the various social systems. Yet no single aspect of primate field studies has less supportive data than the generalizations concerning the survival value of the various presumed antipredator mechanisms. The primate troop can and does exhibit antipredator behavior. Emphasis on different patterns (including vigilance, alarm calls, distraction displays, mobbing, and attack) may vary between species and between age classes and sex classes within a species (44).

Only a few individuals in a troop need spend a great percentage of their time in vigilance for all members of the group to be benefited; typically subadult and adult males perform this role. Visual scanning from high positions may serve to locate intruding conspecific males as well as predators (37, 49), and troop members may be warned of the presence of a predator by alarm calls. The manner in which monkeys respond to a potential predator depends partly upon their own size and mobility and partly upon the relative size and position of the predator.

The jumping and vocalizations of adult males are common alarm behaviors, and are described for such diverse primate species as terrestrial *Erythrocebus patas* (37) and arboreal *Presbytis senex* (19, 74). It is generally considered that such behavior distracts the predator while the females encumbered by young scatter and hide (44). Protective males typically position themselves between the group and a terrestrial predator.

Mobbing, another alarm behavior, requires the presence of a group. A predator may be harried through vocalizations, group defecation and urination (46, 69), and, in large species, branches that may fall from the weight of leaping adult males (*Presbytis*) or be purposely broken off and dropped (*Alouatta*, *Cebus*) (46, 69, 91).

If a predator should surprise a troop at short range, individual flight responses may scatter troop members in various directions, thus confusing a predator. This confers some selective advantage on group life, even though no altruistic tendencies can be detected.

Unlike the smaller primates, larger species attack outright, and some (for example, gorilla and chimpanzee) are more than a match for even the largest

predators. Baboons exhibit a pronounced sexual dimorphism, and, since the baboons of the genus *Papio* typically forage in large multi-male groups, the larger males can form an effective attack unit and displace a predator. The responses of baboons and chimpanzees to leopards have been studied (106) and have been found to include the use of actual weapons (sticks and rocks) (107).

General Conclusions

When the major radiations in the Old World, New World, and Madagascar are compared with each other, no doubt some of the differences in social structure seen in those species adapted to similar ecological niches will be found to result from phylogenetic differences; that is, the social structures of the ancestral forms have been carried forward in the adaptive radiation of these species. For example, the consistent tendency in lemuroid primates such as *Propithecus* and *Lemur* to show multi-male groups with more males than females, a dominance of females over males, and the segregation of troops into all-male and all-female subgroups does not exist in any known continental species (25, 59). The South American radiation has produced a trend toward male participation in parental care and the formation of pair bonds between given males and females.

Although we can generalize about the selective advantages of primate social structures, we must remember that the history of the population under study, its particular adaptation to local environmental conditions, and the idiosyncratic nature of its dyadic relations (which have been ontogenetically established within the particular group) can result in a great deal of variability in social structure, even within the same species when it occurs in widely differing habitats. Hence, in making generalizations about social structure, we must remember that we are talking about behavioral modes or behavioral medians.

Summary

It has been the custom for ethologists to divide mammalian societies into grades. Each ascending level of complexity denotes an increase in the complexity of interaction patterns among

the members of the group. The multi-male group traditionally represented a high level of social organization, as well as the higher primate norm, but it was defined from early studies on terrestrial primates. What we have tried to show is that the uni-male system occurs in a wide variety of primate species in both the cercopithecoid and ceboid radiations. Furthermore, we have attempted to illustrate that multi-male systems are more apparent than real and that many should be considered age-graded-male systems.

The three proposed classes (uni-male, age-graded-male, and multi-male) of social structure (above the level of the parental family) are gradations and represent an increased complexity based on an increased tolerance among adults at the maximum "sociological" age level. There are only a few species for which the data are sufficient to place them in a class. The multi-male system is apparently a specialized form of social grouping that represents a particular adaptation to terrestrial foraging by intermediate-sized primates. It is readily derived from an age-graded-male system. The multi-male system does not differ profoundly from an age-graded-male system, but the former does allow for increased affiliation and cooperation among adult males.

The uni-male system or the age-graded-male system is favored in arboreal species, both frugivores and folivores. The structure of a species' social organization is more predictable for diurnal, leaf-eating forms than it is for the frugivores. We can correlate an arboreal, diurnal, leaf-eating niche with a species having a social structure that tends toward a uni-male system with a small home range and the employment of chorusing behavior to effect spacing. Such species tend to be sedentary and are typified by *Alouatta*, *Colobus*, and *Presbytis*. It would appear, then, that similar predation pressures (semiarboreal felids probably being most important) and similar foraging problems have forced similar behavioral solutions upon these species.

One should be wary of generalizations concerning the form of social structure for any given species, since social structure may vary with habitat. Similar variations have been noted in response to problems of density and habitat disturbance. Parallel trends can be noted in both the ceboid and cercopithecoid lines of evolution. More nearly accurate correlations will be possible only when we have more data

concerning feeding efficiency and anti-predator mechanisms for a wide variety of species, each studied within a range of habitats.

References and Notes

1. J. F. Eisenberg, *Handb. Zool.* 8 (No. 39), 1 (1966).
2. J. H. Crook and J. S. Gartlan, *Nature* 210, 1200 (1966).
3. J. H. Crook, in *Social Behaviour in Birds and Mammals*, J. H. Crook, Ed. (Academic Press, London, 1970), pp. 103-168.
4. C. R. Carpenter, *Trans. N.Y. Acad. Sci.* 4, 248 (1942); *Hum. Biol.* 26, 269 (1954).
5. In Carpenter's original formulation, he suggested that territorial behavior toward conspecific troops was shown. We now know that such exclusive patterns can be effective without overt fighting, and the generalization can be modified to state that all primate troops appear to have exclusive rights to certain areas of their home range at certain critical times of the year, even though they may share parts of their home range with neighboring troops.
6. T. E. Rowell, *J. Zool. London* 149, 344 (1966).
7. K. R. L. Hall and I. DeVore, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), pp. 53-110.
8. P. Jay, in *ibid.*, pp. 197-249; S. Ripley, in *Social Communication among Primates*, S. A. Altmann, Ed. (Univ. of Chicago Press, Chicago, 1967), pp. 237-253.
9. K. Yoshihara, in *Primates*, P. Jay, Ed. (Holt, Rinehart & Winston, New York, 1968), pp. 217-242.
10. Y. Sugiyama, in *Social Communication among Primates*, S. A. Altmann, Ed. (Univ. of Chicago Press, Chicago, 1967), pp. 221-236.
11. T. T. Struhsaker, *Ecology* 48, 891 (1967); *Univ. Calif. Publ. Zool.* 82, 1 (1967).
12. J. S. Gartlan and C. K. Brain, in *Primates*, P. Jay, Ed. (Holt, Rinehart & Winston, New York, 1968), pp. 253-292.
13. C. R. Carpenter, *Comp. Psychol. Monogr.* 16, 1 (1940).
14. T. Ellefson, in *Primates*, P. Jay, Ed. (Holt, Rinehart & Winston, New York, 1968), pp. 180-200.
15. H. Kummer, *Z. Psychol.*, No. 33 (1957).
16. ———, *Social Organization of Hamadryas Baboons: A Field Study* (Univ. of Chicago Press, Chicago, 1968).
17. I. Bernstein, *Behaviour* 32, 2 (1968).
18. F. E. Poirier, in *Primate Behavior*, L. A. Rosenblum, Ed. (Academic Press, New York, 1970), vol. 1, pp. 251-383.
19. R. Rudran, thesis, University of Ceylon, Colombo (1970).
20. P. Marler, *Science* 163, 93 (1969).
21. G. H. Manley, *Symp. Zool. Soc. London* 15, 493 (1967).
22. P. Charles-Dominique, *Biol. Gabonica* 7, 121 (1971); *ibid.* 2, 347 (1966).
23. J.-J. Petter and C. M. Hladik, *Mammalia* 34, 394 (1970).
24. J.-J. Petter, *Mem. Mus. Nat. Hist. Natur. Paris Ser. A Zool.* 27, 1 (1962).
25. A. Jolly, *Lemur Behavior: A Madagascar Field Study* (Univ. of Chicago Press, Chicago, 1966).
26. P. Leyhausen, *Symp. Zool. Soc. London* 14, 249 (1965).
27. P. K. Anderson, *ibid.* 26, 299 (1970).
28. The objection to the term "solitary" is valid if and only if the term is taken literally. If due consideration is given to the existence of indirect communication and the possibility of the maintenance of reproductive continuity among related members of such dispersed population units (I), then we can maintain the older term; if not, then we may well substitute the more cumbersome term, "dispersed, noncohesive family group."
29. P. Charles-Dominique, *Fortschr. Verhaltensforschung* 9, 7 (1972); R. D. Martin, *ibid.*, p. 43.
30. A. Petter-Rousseaux, *Mammalia* 26, 1 (1962); P. Charles-Dominique and C. M. Hladik, *Terre Vie*, part 1 (1971), p. 3.
31. H. Fischer, *Z. Tierpsychol.* 22, 247 (1965).
32. N. A. Muckenhirn, thesis, University of Maryland (1967).
33. G. Epple, *Folia Primatol.* 7, 37 (1967); M. Moynihan, *Smithson. Contrib. Zool.* 28, 1 (1970).
34. M. Kawabe, *Primates* 11, 285 (1970).

35. W. A. Mason, in *Primates*, P. Jay, Ed. (Holt, Rinehart & Winston, New York, 1968), pp. 200-216.
36. M. Moynihan, *Smithson. Misc. Collect.* 146, 1 (1964).
37. K. R. L. Hall, *J. Zool. London* 148, 15 (1965).
38. J. H. Crook, in *Play, Exploration and Territory in Mammals*, P. A. Jewell and C. Loizos, Eds. (Zoological Society of London, London, 1966), pp. 237-258.
39. —, in *Man and Beast: Comparative Social Behavior*, J. F. Eisenberg and W. Dillon, Eds. (Smithsonian Institution, Washington, D.C., 1971), pp. 235-260.
40. H. Kummer, W. Goetz, W. Angst, in *Old World Monkeys*, J. R. Napier and P. H. Napier, Eds. (Academic Press, New York, 1970), pp. 351-364.
41. The uni-male system may be maintained ontogenetically from a founding pair through the combined processes of internal recruitment by birth and antagonism exercised by the founding adult male toward his sons. The maintenance of such uni-male groupings is paralleled in the Carnivora [D. G. Kleiman and J. F. Eisenberg, "Comparisons of canid and felid social systems from an evolutionary perspective" (paper presented at the First International Symposium on World Felidae, Laguna Hills, Calif., 1971)].
42. In recognition of this fact, Crook has distinguished two grades of "multi-male" social structures (2, 3), but he has not elaborated on his reasons for doing so or on the criteria for separation.
43. J. S. Gartlan, in *Old World Monkeys*, J. R. Napier and P. Napier, Eds. (Academic Press, New York, 1970), pp. 445-480.
44. N. Muckenhirn, thesis, University of Maryland (1972).
45. S. M. Mohnot, *Mammalia* 35, 175 (1971).
46. J. F. Eisenberg and R. E. Kuchn, *Smithson. Misc. Collect.* 151, 1 (1966).
47. L. Klein and D. Klein, *Int. Zoo Yearb.* 11, 175 (1971); J. F. Eisenberg, unpublished data.
48. I. DeVore and S. L. Washburn, in *African Ecology and Human Evolution*, F. C. Howell and F. Bourlière, Eds. (Aldine, Chicago, 1963), pp. 335-367.
49. I. DeVore and K. R. L. Hall, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), pp. 20-52.
50. C. H. Southwick, M. A. Beg, M. R. Siddiqi, *ibid.*, pp. 111-159.
51. K. Imanishi, *Curr. Anthropol.* 1, 393 (1960).
52. M. Bertrand, *Bibl. Primatol.* 11, 1 (1969).
53. W. Dittus, unpublished data (1968-1971).
54. J. H. Kaufmann, *Ecology* 46, 500 (1965).
55. T. Nishida, *Primates* 7, 141 (1966).
56. S. Altmann and J. Altmann, *Baboon Ecology: African Field Research* (Univ. of Chicago Press, Chicago, 1970).
57. K. R. L. Hall, *Proc. Zool. Soc. London* 139, 283 (1962); I. DeVore, in *Classification and Human Evolution*, S. L. Washburn, Ed. (Viking Fund Publications in Anthropology, No. 37, Wenner-Gren Foundation, New York, 1963), pp. 301-319.
58. L. Tiger, *Men in Groups* (Random House, New York, 1968).
59. N. Bolwig, *Mem. Inst. Rech. Sci. Madagascar Ser. A Biol. Anim.* 14, 205 (1960).
60. H. Hendrik, in *Dikdik und Elefanten* (Piper, München, 1970) pp. 70-77; G. M. McKay, thesis, University of Maryland (1971).
61. J. F. Eisenberg, G. M. McKay, M. R. Jainudeen, *Behaviour* 38, 193 (1971).
62. C. B. Koford, in *Primate Behavior*, C. Southwick, Ed. (Van Nostrand, New York, 1963), pp. 136-152.
63. D. S. Sade, *J. Phys. Anthropol.* 23, 1 (1965).
64. M. Kawai, *Primates* 2, 181 (1960); Y. Furuya, *ibid.*, p. 149.
65. T. T. Struhsaker, *Folia Primatol.* 11, 80 (1969).
66. F. Bourlière, C. Hunkeler, M. Bertrand, in *Old World Monkeys*, J. R. Napier and P. H. Napier, Eds. (Academic Press, New York, 1970), pp. 297-350.
67. L. L. Klein, "Ecological correlates of social grouping in Colombian spider monkeys," paper presented at the Animal Behavior Society Meeting, Logan, Utah, 1971.
68. C. R. Carpenter, *J. Mammal.* 16, 171 (1935).
69. —, *Comp. Psychol. Monogr.* 10, 1 (1934).
70. —, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), pp. 250-291.
71. D. J. Chivers, *Folia Primatol.* 10, 48 (1969).
72. N. E. Collias and C. H. Southwick, *Proc. Amer. Phil. Soc.* 96, 143 (1952).
73. J. B. Calhoun, in *Physiological Mammalogy*, W. V. Mayer and R. G. Van Gelder, Eds. (Academic Press, New York, 1963), vol. 1, p. 91.
74. G. Manley, in preparation.
75. W. E. LeGros-Clark, *The Antecedents of Man* (Quadrangle, Chicago, 1960).
76. J. F. Eisenberg and E. Gould, *Smithson. Contrib. Zool.* 27, 1 (1970).
77. A. Walker, in *Pleistocene Extinctions*, P. S. Martin and H. E. Wright, Eds. (Yale Univ. Press, New Haven, Conn., 1967), p. 425.
78. C. M. Hladik, *Mammalia* 31, 120 (1967).
79. —, P. Charles-Dominique, P. Valdebouze, J. Delort Laval, J. Flanzly, C. R. Hebd. *Seances Acad. Sci. Paris* 272, 3191 (1971).
80. T. Bauchop and R. W. Martucci, *Science* 161, 698 (1968).
81. C. M. Hladik and A. Hladik, *Biol. Gabonica* 3, 43 (1967); *Terre Vie*, part 1 (1969), p. 27.
82. G. G. Montgomery and M. E. Sunquist, in preparation.
83. A. Gautier-Hion, *Folia Primatol.* 12, 116 (1970).
84. R. W. Thorington, Jr., in *The Squirrel Monkey*, L. Rosenblum and R. W. Cooper, Eds. (Academic Press, New York, 1968), pp. 69-87.
85. F. V. DuMond, in *ibid.*, pp. 88-146.
86. J. D. Baldwin, *Folia Primatol.* 9, 281 (1968).
87. A. Richard, *ibid.* 12, 241 (1970).
88. C. M. Hladik and A. Hladik, *Terre Vie*, in press.
89. F. P. G. Aldrich-Blake, in *Social Behaviour in Birds and Mammals*, J. H. Crook, Ed. (Academic Press, London, 1970), pp. 79-102.
90. Z. Y. Furuya, *Primates* 3, 41 (1961-62).
91. J. R. Oppenheimer, thesis, University of Illinois (1968).
92. The frugivorous species do not show such uniform trends in social structure. As with the folivores, there is a tendency toward a uni-male situation, but at least two kinds of group organization can be discerned: (i) the cohesive uni-male band, which is generally quite small, 20 members (for example, *Cebus capucinus* and *Cercopithecus mitis*), or (ii) the less cohesive, extended group, in which mother families and age-graded-male units forage independently (for example, *Ateles geoffroyi*), reassemble only from time to time at preferred resting loci, and so on. Although all of these species have long-distance calls, the calls are generally not given in a chorusing fashion and their relation to intraspecific spacing is not well understood.
93. H. E. McClure, *Primates* 5, 39 (1964). It should be noted that, although the gibbons are classically considered frugivores (13), they do feed on leaves at certain seasons of the year (14). It may be that further research will lead to their being classified as folivore-frugivores. If such is the case, their spacing system is more easily comprehensible. See also D. J. Chivers, *Malayan Nature J.* 24, 78 (1971).
94. In *Symphalangus*, the peak number of morning calling sessions heard in June was several times greater than the peak number heard between September and January, the months of minimal calling. The only observation of a newborn was recorded in February. While such evidence is obviously not sufficient to establish a birth peak for this species, it suggests that some breeding did occur in June. Likewise, 2.5 times more calls of *Hylobates* were heard in June than in November and February, the months of minimal calling.
95. J. F. Eisenberg and M. Lockhart, *Smithson. Contrib. Zool.* 101, 1 (1972).
96. S. Ripley, in *Old World Monkeys*, J. Napier and P. Napier, Eds. (Academic Press, New York, 1970), pp. 481-512.
97. C. Jones and J. Sabater Pi, *Folia Primatol.* 9, 99 (1968).
98. N. R. Chalmers, *ibid.* 8, 247 (1968).
99. J. Goodall van Lawick, *Anim. Behav. Monogr.* 1, 165 (1968).
100. K. Izawa, *Primates* 11, 1 (1970).
101. V. Reynolds and F. Reynolds, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), pp. 368-424.
102. G. B. Schaller, *The Mountain Gorilla* (Univ. of Chicago Press, Chicago, 1963).
103. For a theoretical discussion, see J. E. Downhower and K. Armitage, *Amer. Natur.* 105, 355 (1971).
104. R. W. Thorington, Jr., in *Progress in Primatology*, D. Starck, R. Schneider, H.-J. Kuhn, Eds. (International Primatological Society, Frankfurt, 1967), pp. 180-184; T. T. Struhsaker, in *Old World Monkeys*, J. Napier and P. Napier, Eds. (Academic Press, New York, 1970), pp. 365-444; J. P. Gautier and A. Gautier-Hion, *Terre Vie*, part 2 (1969), p. 164.
105. Interspecific antagonisms can occur, however, even between those species that form mixed feeding associations, since the propensity to show interspecific aggression apparently varies with respect to the history between the two populations under study and the distribution of resources in the habitat under consideration. In a broad sense, the density of primate populations, either arboreal or semiterrestrial, may be severely limited by the presence of competitors. It should not be assumed, however, that the most severe competition typically comes from other species of primates. Struhsaker (11) has reported that the major food competitor of *Cercopithecus aethiops* in Kenya is the elephant. This competition results from the fact that, during the dry season, the elephants push over the major species of trees that provide food and refuge for the monkeys.
106. A. Kortlandt, in *Progress in Primatology*, D. Starck, R. Schneider, H.-J. Kuhn, Eds. (International Primatological Society, Frankfurt, 1967), pp. 208-224; — and M. Koj, *Symp. Zool. Soc. London* 10, 61 (1963).
107. Although the members of the group that attack the leopard may act individually, the effect of several adult males charging can be quite intimidating to a potential predator and thereby be a distinct selective advantage for a multi-male social group. Such antipredator maneuvers are generally in the province of males, and those species that tend to show responses of this kind generally exhibit a great dimorphism, with the males being much larger than the females; however, dimorphism is less pronounced in the chimpanzee than in the baboon.
108. W. B. Collins, as quoted by F. Bourlière, in *African Ecology and Human Evolution*, F. C. Howell and F. Bourlière, Eds. (Aldine, Chicago, 1963), pp. 43-54.
109. This article is an expanded version of a talk presented by J.F.E. at the Animal Behavior Society Meeting, Logan, Utah, 1971, and is an outgrowth of fieldwork that has been in progress since 1964. Our primary effort was in Ceylon from 1968 to 1970 (95), but studies were also conducted in Central America and Madagascar (32, 46, 76). In 1967, J.F.E. and Suzanne Ripley formed a research group that studied the Ceylon primates from the standpoints of ecology and behavior. Some eight investigators participated in the project from 1968 to 1971. The adaptive patterns that have emerged will be or are being published by individual investigators (19, 23, 44, 53, 88, 96), and this article does not attempt to synthesize all interpretations. Research was supported, in part, by National Science Foundation grant GB-3545, awarded to J.F.E.; National Institute of Mental Health grant RoIMH15673-01; research grant 686 from the National Geographic Society; and Smithsonian Institution Foreign Currency Program grant SFC-7004, awarded to J.F.E. and Suzanne Ripley. The authors wish to thank D. G. Kleiman for a critical reading of the manuscript.