gation of females toward which the other males were also oriented. Much of the alpha bull's activity involved keeping other males away from the females.

Copulation frequencies (in parentheses, Table 1) show that social rank was highly correlated with breeding success (7). We estimate that four of the highest ranking males (GL, CLS, GLS, and YLN), representing 6 percent of 71 individuals observed in area 17, inseminated 88 percent of the 120 females on that beach. The alpha bull from 29 January to 8 March (GL) copulated more frequently than any other male.

Among the four males that copulated most frequently, high rank was positively correlated with (i) demonstrating dominance over other males, (ii) preventing others from mounting and copulating, and (iii) mounting and copulating without interruption (Table 2).

On the other beach under study, area 3, one individual maintained the alpha position during the entire breeding season. This bull was involved in 73 percent of the copulations observed on area 3.

The extent to which social structure restricted mating to only a few males is illustrated by the combined statistics of the entire island. The four highest ranking males on area 17, plus the alpha bull on area 3, accounted for 123 of 144 copulations observed during the season. Thus 4 percent of the males apparently inseminated 85 percent of the females.

Social hierarchies exist in several mammalian species (8), but the type we observed in male elephant seals is especially comparable to that of domestic fowl (9). In both systems, the hierarchy may be linear, or may show triangular relations. The relations between individuals are stable unless fighting leads to reversals. However, among male fowl, high status confers access to food and roosting and nesting sites as well as to females, whereas in elephant seals the competition during the breeding season relates primarily to females. A male elephant seal shows no preference for a particular site, except one close to the females. As the females shift location, the males follow them. High-ranking males do not eat during the 3-month haul-out, and therefore do not compete for food. In addition, all the male elephant seals in our population exhibited a dominance relation with each other, whereas "no-contest" relations

occur between some individuals in chicken peck orders.

A social system in which only a few males mate might have important genetic consequences for the evolution of the species, particularly if the same males continue to mate for more than one season. We do not know how many seasons one male successfully competes for females, or whether he fertilizes all those with whom he mates (10).

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7. Copulation frequencies include only the first of a female's copulations that we observed. Additional copulations by the same female are excluded because we assumed that insemination occurred most likely as a result of the initial mating.
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10. We attached permanent monel metal tags to many of the seals to identify them in future seasons and study the reproductive rates of males and females.
11. Our studies in Año Nuevo State Reserve were authorized by the California Department of Parks and Recreation, W. P. Mott, Jr., director; and permission to tag seals was granted by the California Department of Fish and Game, W. T. Shannon, director. We acknowledge the field assistance of M. Skeel, D. Ramsey, G. Eaton, and R. Gentry.

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Colobus guereza: Territoriality and Group Composition

Abstract. *Troops of the black and white colobus* Colobus guereza *in the Budongo Forest, Uganda, average eight animals with a typical composition of one adult male, four adult females, two subadults, one juvenile, and one infant. Solitary males and small all-male groups also occur. Troops of mixed sexes have well-defined territories which coincide roughly with the home range. Territories of five groups averaged 0.062 square mile (0.137 km²) in area, agreeing closely with territory-sizes of Asian Colobine monkeys. Adult males have a roar that is concerned with maintaining territorial spacing, but not with actual territorial defense. The territories of these arboreal, forest animals are much smaller than the home ranges of more terrestrial and nonterritorial open-country primates.*

Among the Colobine monkeys of the Old World, the gray langur, *Presbytis entellus*, seems to be territorial, at least in certain areas (1). In Africa, two investigators have reported territoriality in the black and white colobus monkey *Colobus guereza* (2, 3). The black and white colobus, observed in the Budongo Forest, Uganda, at irregular intervals between 15 October 1964 and 27 May 1965, moved in the tree tops in close-knit groups averaging 8 animals in the 14 troops accurately counted, with a range from 2 to 13 individuals. In an average troop there is a single adult male, four adult females, perhaps one subadult male and a female, a juvenile, and perhaps one infant. There are rather smaller troops

in the southern part of the Queen Elizabeth National Park but with a similar basic composition (Table 1). Solitary males and small all-male troops are difficult to detect and may be more common than our two cases indicate. Ullrich (2) describes a troop of 13 animals in Tanzania with the same composition. Schenkel and Schenkel-Hulliger (3) report on four troops in Kenya, two containing 6 animals, one 12, and one 15 animals. The numbers of adult males and females indicated are equal, whereas we found a preponderance of females. However, they do not distinguish between adults and subadults. Some variation may be a result of differences in the criteria for sexing animals. Ullrich mentions sex difference in

Table 1. The composition of 14 troops of black and white colobus in the Budongo Forest, Uganda, and five troops at Ishasha in the Queen Elizabeth National Park, Uganda.

Total individuals	Adults		Subadults			Juveniles: black-white	Infants: white
	Males	Fe-males	Males	Fe-males	Un-sexed		
Budongo							
11	1	5	–	1	3	1	–
11	1	5	–	–	3	1	1
9	1	5	1	–	–	2	–
2	1	–	1	–	–	–	–
9	1	3	–	–	3	2	–
13	1	6	1	–	3	2	–
4	1	2	–	–	–	1	–
6	1	3	1	1	–	–	–
13	2	5	–	3	–	–	3
8	1	4	1	1	–	1	–
11	3	4	2	1	–	1	–
8	1	4	–	1	–	1	1
7	1	3	–	1	–	2	–
5	1	2	–	–	–	2	–
Queen Elizabeth National Park							
5	1	2	1	1	–	–	–
1	1	–	–	–	–	–	–
3	2	1	–	–	–	–	–
9	1	4	–	1	1	2	–
8	1	4	1	–	–	2	–

urine-staining on the tail which we were unable to see. In Uganda, animals were readily sexed by a difference in the white patch below the tail which is a complete ring in males and a broken ring in females.

Each group of colobus defended the boundaries of its home range against other troops, so that home range and territory virtually coincide, apart from short transgressions across the boundaries. The home range is the area in which the troop moves during the year, the territory is that part of the home range which is actively defended through repulsion of intruding troops by vocalization, display, or combat. Estimates of territory sizes in five colobus troops measured in square miles (1 km^2 = 0.3861 sq. mi.) are 0.036, 0.038, 0.075, 0.077, and 0.084. The average is 0.062 square mile. Ullrich (2) estimates territory size of one colobus troop in Tanzania at 0.058 square mile. Schenkel and Schenkel-Hulliger do not report territory size of colobus in Kenya, but from their sketch-map I calculate that the five territories shown are even smaller, ranging from 0.004 to 0.013 square mile. All available estimates of territory size in the black and white colobus give an average of 0.037 square mile, similar to the average reported for langur territories of 0.034 square mile excluding non-territorial populations (1–5). Recorded territories of other primates range from 0.002 to 0.50 square mile in area (6–10).

Territorial organization results in a distinctive pattern of distribution of colobus troops through the forest—they are more uniformly dispersed than would be expected by chance. Some mechanism is required to maintain the pattern of distribution. A different mechanism is needed to correct any change in the pattern such as might result when one troop seeks to invade the territory of another. One such mechanism is territorial defense (11). These two functions will require signals with rather different properties. For maintaining intertroop distance, a signal is needed which can readily be perceived over the normal range between troops. For forest animals visual signals can only be perceived at close range. Sounds are the obvious solution. Colobus possess an ideal signal for such a function in the "roaring" of adult males. This sound is very loud, audible for at least 1 mile, well beyond the average intertroop distance found in the Budongo Forest. To be accurately identified by adjacent troops in the face of noise from wind and other forest animals, the sound must have a distinctive structure. Male roaring has a well organized temporal pattern. The basic unit is a phrase of approximately 7 to 15 syllables or compound pulses with an average duration of about 0.7 second. Each syllable is composed of two to four brief pulses, about 10 msec in duration given in a rapid sequence. The energy in each pulse tends to be grouped in two frequency bands centered around 600 and 1200 hz, with varying emphasis on one band

or the other. Intensity of the syllables usually reaches a maximum in the middle of the phrase. The first phrase in a sequence is usually preceded by an explosive snort which includes frequencies across a wide spectrum, but with the main energy between 1500 and 2000 hz. It is sometimes drawn out into a train of faint pulses (Fig. 1, A2). Low-intensity roaring commonly consists of a snort and a single phrase, repeated at intervals of several seconds. In more intense roaring, the phrases are commonly grouped in sequences of four with a snort before the first one. The second is often the louder, with a faster syllable rate than the others. The final phrase is often deeper pitched than the others as a result of weak emphasis of the upper frequency band. In the most intense display, loud sequences of up to 20 or more phrases may be given in rapid succession, with intervals of 0.2 second between them. Sequences lasting 20 minutes have been recorded. The roaring is often accompanied by a vigorous display in which the male leaps rapidly from branch to branch in a high tree with sufficient impact to shake branches and to dislodge dead snags.

Roaring has a number of characteristics that correlate with the function of maintaining intertroop distance. It often begins spontaneously, which is a requirement for a behavior pattern which is concerned with maintaining an existing condition. Once roaring has started it is contagious, triggering calling in adjacent troops. From a good vantage point, roaring can be heard spreading through the forest in a wave from troop to troop. It is especially common at dawn and dusk, and often occurs during the night as well. It is likely to emanate from favorite sleeping trees within the territory. Colobus and other monkeys are known to be faithful to particular sleeping trees over periods as long as 5 years (12, 13). Male roaring has additional functions, including intimidation of predators, and with some impact on relationships within the troop, but maintenance of a pattern of intertroop spacing is probably primary. Other territorial, forest-living monkeys have an analogous vocalization which is loud and far-carrying, with a more or less extended pattern in time including the "morning calls" of male and female gibbons *Hylobates lar* (7, 8) and the "whoop" call of adult male langurs (5). The gobbling call of titi monkeys *Callicebus moloch* shares many of these characteristics (9), and the classical parallel is the roaring of male howler

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monkeys *Alouatta palliata* in Central America (*10, 14*) which is similar in physical structure to the roaring of the black and white colobus, so much so that it is tempting to think of it as an example of convergent evolution in behavior (Fig. 1, E and F).

Although male colobus roaring is concerned with maintenance of the pattern of territorial spacing of troops, it is not used in active defense of the territory against intrusion (*3*). As a first response to territorial intrusion, some individuals will advance to a position where the intruders can be clearly seen and sit in a crouched posture glaring fixedly at them, often clicking tongues as they do so. The mouth is suddenly opened wide with the teeth covered by the lips, and the tongue is clicked from roof to floor of the mouth making a soft smack. Adults of both sexes were seen
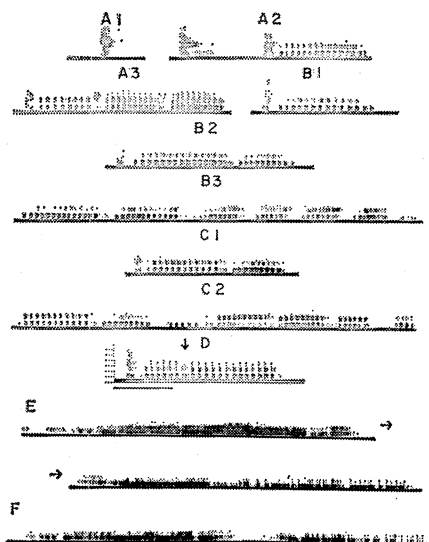

Fig. 1. Sound spectrograms of the roaring of adult males of the black and white colobus in Uganda (*A–D*) and the red howler monkey *Alouatta seniculus* in Trinidad (*E* and *F*). (*A1*) Single snort. (*A2*) Snort with pulsed structure followed by a snort and a single low-intensity phrase of roaring. (*A3*) Three phrases of roaring each preceded by a snort. A1–3 are the same animal. (*B1*) Single phrase of second individual preceded by snort. (*B2* and *3*) Two and seven phrases from more intense roaring of the same animal. (*C1* and *2*) Similar records of roaring of a third male. Note the lack of obvious individual differences. (*D*) Two males roaring against each other. Start of the second is indicated by the arrows. (*E* and *F*) Samples of low intensity roaring of a male red howler monkey recorded by F. Nottebohm on Bush Bush Island, Trinidad. Only at low intensity can this pulsed structure be detected which so closely resembles colobus roaring. The center section of *E* is more typical of intense roaring. *D* includes a time marker of 0.5 second and a frequency scale marked at 500-hz intervals.

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tongue clicking in such circumstances. In males, erection of the penis can sometimes be seen and must be visible to the intruders. In response to further intrusion, an adult male will begin leaping noisily from branch to branch toward the other troop, slapping on branches as he alights, and often dislodging twigs and dead snags which crash to the ground. Occasionally he will take an immense leap from a high branch, falling 20 to 30 feet (about 6 to 9 m) into the understory with a loud crash, then climb back up and repeat the sequence. At close range the combatants may feint with their hands, but no contact was ever seen. After engaging in such exchanges for several minutes, the intruders will withdraw. Only at this stage is roaring sometimes given, after the territorial spacing has been restored. In common with most other territorial animals, the adult males take primary responsibility for active defense of the boundaries. Moreover, when the troop contains more than one adult male, it is normally the dominant one in the hierarchy who plays the major role, although others may show milder displays at the same time. Only the top ranking male seems to be responsible for the roaring, although other adult and subadult males were sometimes heard giving the snort which normally introduces roaring. There is considerable tension between the several adult males in a troop, and a dominance hierarchy can be discerned. Tension between females was much less marked and no hierarchy could be detected.

Thus, colobus monkeys possess different sets of signals for maintaining intertroop distance and for increasing the distance between troops after an intrusion. The same can be said of other forest-living territorial monkeys. On the other hand, there are primates which seem to lack any conspicuous signals for maintaining intertroop distance. The lack is particularly obvious in the nonterritorial primates such as macaques, baboons, and the patas monkey *Erythrocebus patas* which tend to leave the forest environment and to invade more open habitats (*15, 16*). Along with this trend toward loss of territoriality is a great increase in the size of home range (*17*). Given a home range which may be as large as 15 square miles (39 km²), effective defense of the whole area, or of a significant fraction of it as a territory, would be very difficult to accomplish. The home ranges of adjacent troops often overlap extensively. Although

some portions of the home range of a troop, the core areas, are usually free of intrusions by other troops, these semi-terrestrial primates seem to rely more on casual visual contacts than on displays or vocalizations to maintain whatever uniformity there may be in the spatial distribution of troops. When the home range exceeds a certain threshold value, perhaps somewhere around one square mile, territoriality in the usual sense may disappear. Above this value, the very rarity of intertroop contacts would make territoriality difficult to maintain.

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