

Territorial Behaviour in the Green Monkey, *Cercopithecus sabaues*: Seasonal Defense of Local Food Supplies

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Summary. Territorial behaviour among green monkeys (*Cercopithecus sabaues*) was studied for 15 months in Senegal, West Africa. Intergroup relations were quantified, as well as the distribution and availability of resources in the heterogeneous habitat. Intergroup encounters varied seasonally in their location and frequency. Green monkeys did not specifically engage in territorial 'patrols', but rather, areas of range-overlap with neighbouring groups were exploited for specific resources they contained. Neighbours showed flexible responses to seasonally variable competition for these resources. Four types of encounter were quantified, varying in intensity and duration, with descriptions of the ecological context underlying each: chance, ritual, one-sided, and intense encounters, varying according to the relative net benefit to each group to defend specific resources. This depended on the relative availability and distribution of these resources, and the degree to which they could be depleted. Comparisons were made with other populations of *C. aethiops*. A higher frequency of encounters was associated with higher population density at one site, and with monkeys living in ranges small enough to be economically defensible.

Introduction

There is evidence for many functions of territoriality in animals (Davies 1978). Several may be particularly pertinent to primates: to reduce competition for mates, to reduce risks of being preyed upon by dispersing the population, and to protect local supplies of food. In this paper, I shall consider the last of these in detail, with particular reference to Brown's (1964) concept of economic de-

fendability: a territory should only be defended if the benefits of defense exceed the costs.

With increasing numbers of field studies of primates, there is better scope for inter- and intraspecific comparison of territorial behaviour, which can often best be understood using comparative ecological data. Fruitful comparisons have been made among the closely related 'savanna' baboons, *Papio* sp., where variability in intertroop relations has been shown (reviewed in Anderson 1981). Differences in habitat were shown to account for differences in territorial behaviour among chacma baboons (*Papio ursinus*), and seasonal changes in resources at one location were also shown to affect intertroop relations (Hamilton et al. 1976). Similar variability between populations has been shown among the smaller African savanna monkey, the super-species *Cercopithecus aethiops* (Gartlan and Brain 1968; Kavanagh 1981). Details of the ecological factors involved, however, are poorly quantified. In addition, there has been no study of seasonal variability in territorial behaviour among *C. aethiops*. This would provide an important alternative method of elucidating the role of the distribution and availability of resources on intergroup relations.

This paper examines the dynamics of territorial behaviour in the green monkey, *Cercopithecus (aethiops) sabaues*, with careful attention to ecological detail and seasonal fluctuation in resources. There are several factors concerned with ranging behaviour and relationships between groups that should be made clear. 'Home range' covers any area that animals use (monthly, seasonally, annually); various grades of 'core area' may be defined according to different levels of intensity of use; 'territory' as originally defined by Burt (1943) refers to any area defended from others of the same species; 'exclusive territory' refers to the

area into which others are never allowed to enter (Jolly 1972). These are useful distinctions in studying territorial behaviour, but as will be discussed in this paper, they may be arbitrary distinctions within a flexible system of land and resource partitioning, with a variable set of costs and benefits to defending resources.

Materials and Methods

These have been fully described elsewhere, together with other aspects of the behavioural ecology of the green monkey (Harrison 1982, in press, in preparation). In summary, the study was carried out in the Parc National du Niokolo-Koba in Senegal, West Africa, between October 1978 and December 1979. Four sympatric species of diurnal primates occurred at Mt. Assirik, the main study area of the Stirling African Primate Project: chimpanzees (*Pan troglodytes verus*), baboons (*Papio papio*), patas monkeys (*Erythrocebus patas*), and green monkeys, which formed the subjects of SAPP's long-term synecological study.

The vegetation around Mt. Assirik is a mosaic of woodland (37%), grassland and bamboo (32%), open laterite plateau (28%), and narrow strips of gallery forest (3%) which grow in steep-sided valleys that cut through the laterite. Part of one such valley, Lion Valley, was the core ranging area of the study group of green monkeys.

The dry season, without rain from November to May, is sharply defined from the wet season, June to October (mean annual rainfall, 1976–1979, 954 mm). The cycles of production of important species of fruit and flowers (the major element in the green monkeys' diet, see Harrison 1982, in preparation) were not simply correlated with season. The availability and distribution of these species were systematically recorded: important plant-species were defined as those constituting at least 5% of any month's sampled diet. The distribution of important species was recorded in terms of their presence or absence in each of 2,854 quadrats (25 m × 25 m) in the monkeys' home-range. An index of the degree of clumping in the distribution of each species was calculated: for every quadrat that contained a particular species, I counted the number of the surrounding 8 quadrats that also contained that species. The 'index of clumpedness' was the mean number of surrounding quadrats that contained the focal species. A low number suggested a species occurring in isolated groups of quadrats, whereas a high number suggested a more continuous, even distribution. The proposed index measures clumpedness both locally and over wider areas. The local density of each important species was recorded from a sample of 30 quadrats containing that species. The projected area of tree canopy was sampled from 15 trees of each species, and used as a measure of the food-producing area. The phenology of important species was also monitored: when fruit or flowers of a species were an important component of a month's diet, the percentage of trees of a species that had fruit or flowers available to the monkeys was quantified from a sample of 50 trees. The total amount of fruit and flowers available each month was calculated by summing the amounts of each important species for that month. Totals varied between 2,766 m² of projected canopy area in November and 44,844 m² in January (Harrison 1982, in preparation).

A single group of green monkeys was chosen for the focus of the study (Camp group). The group varied in size from 18 to 28 members (mean 25.5), depending on births, deaths, and the migration of adult males. There were 7 adult females with their offspring, 2 sub-adult males, and between 3 and 6 adult males. The group occupied a home-range of 1.78 km².

Two estimates of the density of green monkeys were calculated. The local density was 14.3 monkeys/km² (Camp group), reflecting the level of competition for available resources. The overall population density was 4.4 monkeys/km² (11 or 12 groups in 50 km² around Mt. Assirik, with mean group size 19.2). The latter estimate more closely reflects the carrying capacity of the habitat, and differs from the former because of the heterogeneous mosaic of vegetation-types, some lacking suitable resources, that comprises the habitat at Mt. Assirik.

The behaviour of individuals in Camp group was sampled during 5-day, dawn-to-dusk sample-periods each month. During each 5-day sample the location of the group was mapped every 30 min, and details of the activity of each individual in view were systematically recorded using instantaneous scan-sampling (Altmann 1974), at 15-min intervals. Maps were divided into 25 m × 25 m quadrats, so that various patterns of range-use and vegetation could be quantified. All intergroup encounters were recorded and mapped; those occurring during 5-day samples give an estimate of their frequency. At each encounter, as full a description as possible was made of the monkeys' behaviour and the prevailing ecological circumstances. All occurrences of the noisy displays of adult males, and the duration of each encounter could be scored reliably, as could the detailed mapping of locations and the group's movements. Durations of encounters were measured by the following criteria: an encounter started when each group became aware of the other's presence, as signalled by vigilance, vocalizations, or displays; an encounter ended if one group moved away, or if members of each group ceased to pay attention to the other. Individual identities of participants were noted whenever possible but are not analysed here, since the fast action and poor visibility at encounters gave unreliable data using such opportunistic sampling.

Results

Home Range Overlap

Camp group's home-range was centred on Middle Lion Valley. There were three neighbouring groups, with whom Camp group had aggressive encounters in areas where their ranges overlapped. The main competing neighbours were CMM group, whose range included the forest upstream of Camp group, and D group which ranged downstream. The third, AV group, was less commonly encountered, since its range bordered that of Camp group in a less commonly used stretch of woodland (Fig. 1).

These three groups used areas that overlapped Camp group's total home-range (2,854 25 m × 25 m quadrats) by 74, 124, and 75 quadrats respectively. These 273 quadrats of home-range-overlap (17 ha) represent 9.6% of Camp group's range, and are henceforth referred to as overlap-quadrats. Since neighbouring groups were not followed systematically, these figures may be underestimated.

The use of overlap-quadrats by Camp group was calculated from ranging maps and scan-sampling data: 13.7% of quadrats (219 of 1,598) used during 5-day samples were in the overlap-zone,

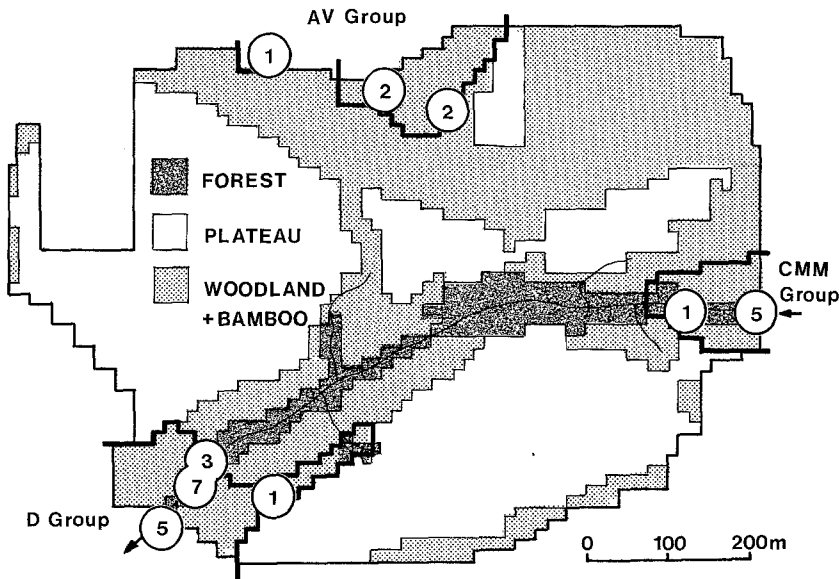


Fig. 1. Home range of Camp Group, showing areas of range-overlap (within heavy lines) with neighbouring D, CMM, and AV Groups. White circles show the location and frequency of intergroup encounters. The forest follows the streambed of Lion Valley, arrows indicate the direction of flow

while 17.3% of time (1,508 of 8,700 $1/2$ -h intervals) was spent in these quadrats. Temporal and spatial selection ratios may be calculated as measures of whether overlap-quadrats were used more than expected by chance during 5-day sample (s.r. = %observed/%expected, in which a ratio of one is chance):

spatial selection ratio = $13.7/9.6 = 1.4$;

temporal selection ratio = $17.3/9.6 = 1.8$.

Both ratios show that overlap-quadrats were used more than expected by chance. However, selection of these quadrats was not as strong as selection for certain habitat-types (see Harrison 1982, in preparation). For example, spatial and temporal selection ratios for gallery forest quadrats were 4.8 and 7.7 respectively. Thus, the selection of particular habitat-types during daily travel confounds the issue of selection of overlap-quadrats. Table 1 shows the number of overlap-quadrats in each habitat-type, and how many of these that were used during 5-day samples. Virtually all of the overlap-quadrats in closed-canopy vegetation (gallery, closed woodland, scrub) were used, but not the quadrats in open vegetation (open woodland, plateau). This was the trend for habitat selection demonstrated in Harrison (1982, in preparation), i.e., that closed-canopy vegetation was chosen in preference to open vegetation. Thus, over the year the monkeys were not using overlap-quadrats more than expected from their preference for particular vegetation-types. In other words, the green monkeys did not engage in regular 'border patrols' along their territorial boundaries.

Table 1. Habitat-types of quadrats in range overlap-zones (N), and use of these quadrats during 5-day samples (N -used)

	N	N -used	%
Gallery forest	37	37	100
Closed woodland	19	19	100
Bamboo	39	37	95
Scrub	10	8	80
Open woodland	157	118	75
Plateau	11	0	0
Total	273	219	

Intergroup Encounters

No intergroup encounter at Mt. Assirik was characterised by vocalizations alone, nor did any encounters involve 'friendly' mixing of groups. Encounters started in various ways: when approaching a boundary, adult males moved ahead of others to investigate; or, upon sighting a neighbouring group, females or immatures gave specific calls (long rrrr rrrr calls) which alerted others to the presence of neighbours; or rarely, surprise encounters in thick vegetation elicited barking from adult males, and females and young gave 'chutter' calls, and most monkeys ran towards the commotion.

This was followed by displays, and sometimes chases, by adult males. Displays involved ritualized 'leaping and crashing' through the canopy, ricocheting off branches while jumping from tree to tree, finally dropping to land noisily in dense foliage. These impressive bouts of 'leaping and crashing' were interspersed with vigilant males

from each group facing each other, giving silent, long-distance (5–40 m) displays of their white chests, jerking penile erections, and canines. These displays often led to further ‘leaping and crashing’ chases. However, no physical contact between opposing males was observed during intergroup encounters.

Participants in encounters were almost exclusively adult males. Younger males rarely engaged in the visual displays, but not in chases or ‘leaping and crashing’. The rest of the group stayed on the ground and took no part. Generally females and young were relaxed, often continuing to feed, groom, or play beneath the noisy arboreal displays of the males, although all seemed to be aware of the focus of any encounter, and remained a cohesive group.

The above describes the monkeys’ behaviour during intergroup encounters in gallery forest or closed woodland, where 24 of the 27 observed encounters took place. The other three occurred in open woodland or bamboo and took a different form. Most notably, all age/sex classes except infants took part: this involved skirmishes on the ground between opposing phalanxes of monkeys rushing and slapping out at each other, or adult males chasing each other on the ground. Throughout, females and youngsters kept up a chorus of ‘chuttering’. Groups remained tightly bunched, and the encounters were brief (less than one minute). The key factor seemed to be the lack of continuous canopy in which males could carry out their ‘leaping and crashing’ displays, as the ritualized expression of intergroup aggression.

The 27 intergroup encounters observed throughout this study form the basis of analysis (16 with D group, 6 with CMM group, and 5 with Assirik Valley group). To measure the frequency of territorial encounters, only those occurring during 5-day samples are considered: 15 encounters during 60 all-day observations gives an average rate of one encounter with any of the three neighboring groups every four days; or, an encounter with the same group every 12 days. Encounters tended to occur in bursts, however, on successive days, between longer lulls without encounters; the longest gap between observed encounters was two months.

Seasonal Variation in Territoriality

During 5-day samples, 4 intergroup encounters occurred in the 7-month dry season, compared with 11 encounters in the 5-month wet season (i.e. on average, one encounter every 8.8 days in the dry

Table 2. Seasonal use of overlap-quadrats, in space and time, during monthly 5-day samples

		% of monthly quadrats	% of monthly time-periods	No. of encounters	
Dry	November	12	9	0	
	December	16	13	1	
	January	14	13	0	
	February	15	31	0	
	March	13	13	0	
	April	7	11	1	
	May	11	22	2	
Wet	June	11	15	2	
	July	11	13	1	
	August	25	30	3	
	September	19	30	4	
	October	18	22	1	
		Overall means		Totals	
Dry season	13%	$U=11$	16%	$U=10$	4 (1/8.8 days)
Wet season	17%	n.s.	22%	n.s.	11 (1/2.3 days)

season, and one every 2.3 days in the wet season) (Table 2). There was a corresponding seasonal trend in the monkeys’ use of overlap-quadrats, both in space and time, but in neither case is this significant (Mann-Whitney, Table 2). There was a positive correlation, however, between temporal use of overlap-quadrats and frequency of intergroup encounters ($r=0.61$, $P<0.05$). The same trend was seen for spatial use of overlap-quadrats, but this just fails to reach statistical significance ($r=0.48$, $0.05<P<0.1$). Thus, more intergroup encounters were associated with more intensive use of overlap-quadrats, which tended to occur more in the wet season.

Ecological Context of Intergroup Encounters

Camp group’s range expanded and contracted according to food availability and distribution, and the degree to which resources could be depleted (see Harrison 1982, in preparation). Four different types of intergroup encounter were distinguished, which depended upon the prevailing ecological circumstances: chance, ritual, one-sided, and intense.

Chance Encounters. These were chance meetings between groups, at unexpected locations, with brief displays and mutual avoidance ($n=5$, 18% of encounters). The encounters were unpredictable in terms of their past history at these locations, where there were no specific resources to contest. Typi-

cally these encounters occurred in less frequently used areas of woodland.

Ritual Encounters. These were ritual meetings between groups, on established territorial boundaries, near a limited but shared, non-depletable resource such as water ($n=9$, 33% of encounters). They involved brief and relaxed displays from adult males, and mutual tolerance either side of an accepted border. For example, in the late dry season a solitary water spring became a focal resource at the border between the ranges of Camp and D groups (see Fig. 1). Although limited in distribution, such a resource could not be depleted by use, and exclusive access was of no advantage to either group, given the cost of defense. A boundary running through the spring was established, allowing shared access, and maintained by brief, relaxed, ritual displays from adult males each time groups met near the spring.

One-Sided Encounters. One-sided encounters occurred in areas containing resources that were important for one group but relatively unimportant for the other ($n=9$, 33% of encounters). Encounters involved the former group aggressively supplanting the latter, whose members retreated into home territory without resistance. Important resources in these cases were clumped, rare, and significantly depleted by use, such as prized fruit trees with limited distribution or which cropped badly, and which were therefore worth defending for exclusive access.

For example, the highly prized fruit of *Pseudospondias microcarpa* had a very restricted distribution, growing only near permanent water. Along the streambed in Camp group's range there were approximately 90 *P. microcarpa* trees (Fig. 2 and Table 3), while in the exclusive territories of D and CMM groups there were three trees and one tree respectively. There was strong pressure for these neighbouring groups to expand their ranges and aggressively maintain exclusive access to the *P. microcarpa* trees in the areas of overlap with Camp group's range. In contrast, there was no pressure on members of Camp group to defend these areas, or to prevent encroachment by their neighbours, since *P. microcarpa* was common elsewhere in their range (phenological samples (March): 58% of *P. microcarpa* trees fruiting, giving approximately 55 trees containing ripe fruit in their range). Through February and early March, before the fruit had ripened, there was a series of one-sided intergroup encounters between Camp group and each of the neighbouring groups ($n=4$ observed).

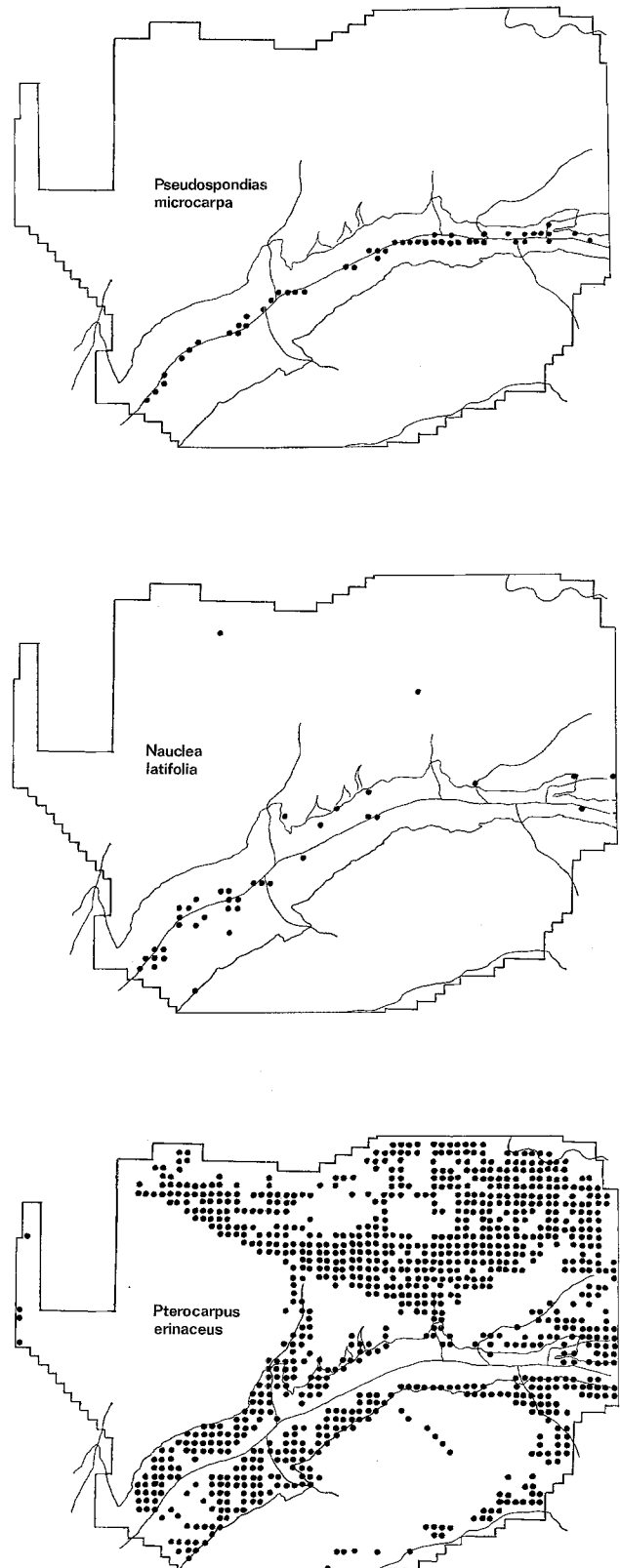


Fig. 2. Distribution maps of three important food-species within Camp Group's range: *Pseudospondias microcarpa*, *Nauclea latifolia*, and *Pterocarpus erinaceus*. Dots show the location of every quadrat containing the relevant species

Table 3. Summary data on the availability and distribution of three major food-species in the diet of the green monkeys, pertinent to intergroup relations (see text)

Species	N of quadrats	Local density (trees/quadrat)	Clump. index	Phenology % fruit (month)
<i>Pseudospondias microcarpa</i>	50	1.9	2.2	58% (March)
<i>Nauclea latifolia</i>	38	1.3	1.6	89% (August)
<i>Pterocarpus erinaceus</i>	995	3.6	5.5	56% (January)

During each of these, Camp group retreated from the advancing, aggressive displays of adult males from D and CMM groups. During this period, there were no other important resources in these areas that could explain such behaviour, suggesting that the ripening crop of *P. microcarpa* fruit was their major concern. Throughout this period, all groups regularly tested *P. microcarpa* fruit for ripeness by feeling, smelling, and test-biting selected fruits.

By March, the range of Camp group had contracted as a result of the earlier encounters, and D and CMM groups moved more consistently into the areas of range-overlap to feed on *P. microcarpa* fruits. The gain for these groups was high, yet the cost to Camp group of temporary withdrawal from these areas was low. Throughout the fruiting season (March-early April), no further encounters were observed. Camp group's range expansion at the end of the *P. microcarpa* crop provided further evidence for the resource-dependent nature of territorial boundaries and intergroup encounters in these monkeys. These one-sided encounters were not the result of fixed dominance relationships between groups, as for example in *Colobus badius* (Struhsaker and Oates 1975) and *Papio ursinus* (Hamilton et al. 1975). On other occasions, Camp group successfully supplanted both of its neighbours.

Intense Encounters. Intense, mutually aggressive encounters occurred over resources that were important to both groups, such as scarce, depletable, fruit trees ($n=4$, 15% of encounters). Both groups gave intense displays and aggressive chases, and encounters were long and noisy, both in terms of vocalizations and 'leaping and crashing' displays.

For example, the fruits of *Nauclea latifolia* were uncommon (Table 3), yet important in the diet,

occurring at a time when no other 'primary choice' foods (fruit or flowers) were available (Harrison 1982, in preparation). Although 38 quadrats in Camp group's range contained *N. latifolia* (see Fig. 2), fewer contained individuals that bore good crops of fruit. In the overlap-zone between Camp and D groups, 9 quadrats contained good specimens: in other words, even ignoring the quality of the resource, about 25% of all *N. latifolia* in Camp group's range was concentrated in the area of overlap with D group. *N. latifolia* was equally scarce throughout D group's range. Thus, heavy use of the overlap-zone by both groups was expected, with both being keen to defend a certain proportion of the focal resource for exclusive access, given the potential depletion with shared access.

In August, as *N. latifolia* ripened, the first intergroup encounter occurred at the upstream side of the 124-quadrat overlap zone, at the edge of Camp group's exclusive territory (see Fig. 1). The encounter was ritual and relaxed (type 2), and Camp group made no attempt to move further downstream. The following day there was another encounter 150 m further downstream. On meeting, both groups erupted into violent chasing and fierce 'leaping and crashing' displays – an intense, type 4 encounter. This lasted for 2 h and 20 min, before Camp group moved upstream. Three days later, another intense encounter took place, lasting 2 h and 30 min. This took place mid-way between the previous two encounters, suggesting that a temporary boundary was emerging, to divide this crucial stand of *N. latifolia* between the groups. The monkeys subsequently fed extensively from the *N. latifolia* on respective sides of this boundary.

Absence of Encounters

Analysis of the ecological conditions under which no intergroup encounters occurred further clarifies the important qualities of resources that influence territoriality. The longest period without observed encounters was from mid-December to mid-February. This period coincided with the cycle of flower buds and flowers of *Pterocarpus erinaceus*, the most widespread tree species in the region, which made up over 50% of the monkeys' diet in January (Fig. 2 and Table 3). *P. erinaceus* flowers were equally abundant for neighbouring groups. Thus, there was no possible localized competition between groups for the major food resource during this period, nor for any less important resources, and no intergroup encounters occurred.

It is not simply the overall availability of any food that determines whether or not it is a poten-

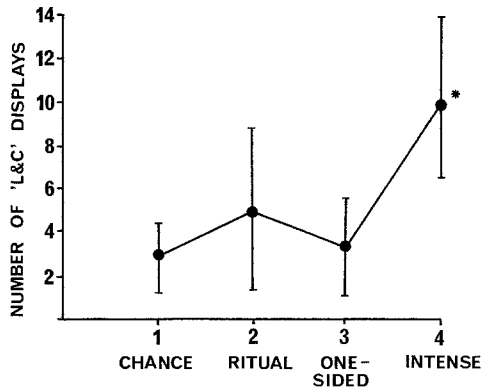


Fig. 3. Mean number of 'Leaping and Crashing' displays during each type of intergroup encounter, with standard deviations. The asterisk marks the statistically different mean ($P < 0.05$)

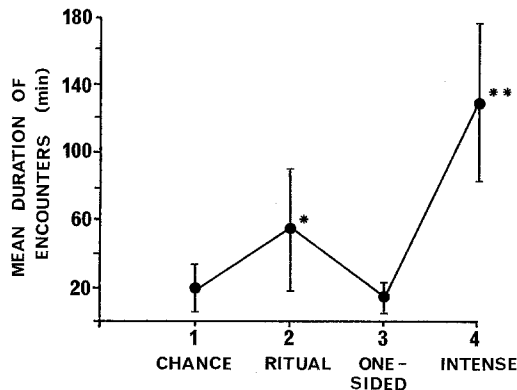


Fig. 4. Mean duration (in min) of each type of intergroup encounter, with standard deviations. Asterisks as in Fig. 3

tially competitive resource, but more particularly its distribution and relative importance to either competitor. There was no correlation between overall food availability and the number of intergroup encounters ($r = -0.17$, n.s.).

Number of Displays and Duration of Encounters

Two quantifiable measures were taken during intergroup encounters which lend support to the independently derived, qualitative distinctions between types of encounter: the mean number of displays and the mean durations for each type of encounter (Figs. 3 and 4).

Analyses of variance of the number of displays per encounter, and of the durations of encounters show significant differences (Anova: $F = 5.0$, $P < 0.01$; $F = 14.4$, $P < 0.001$, respectively). Post hoc comparisons of means (Least Significant Differences, $P < 0.05$) show that intense encounters had significantly more displays and lasted longer than other types of encounter. Ritual encounters lasted

longer than chance or one-sided encounters, although there were no differences in the number of displays between these three types.

In summary, chance encounters involved very few displays, and through mutual avoidance, ended quickly. One-sided encounters ended as quickly, and one group supplanted the other with as few displays. Ritual encounters lasted much longer, but also involved a small number of displays per encounter (although this represents far fewer displays per unit time, in keeping with their milder nature). Intense encounters involved most displays and lasted far longer than other encounters.

Discussion

What emerges from this analysis is that territorial behaviour in the green monkeys at Mt. Assirik is not a rigid maintenance of fixed boundaries, but a flexible response to seasonally variable competition for resources. This is reflected in four types of intergroup encounter, which range from mutual tolerance at certain resources to intense aggression at others. However, this may be a somewhat arbitrary imposition of categories onto a continuous scale of the monkeys' motivation to defend resources, or future access to them. If members of both groups have low motivation to defend a resource (determined by its current distribution and availability), then ritual encounters would be more likely when groups met; if members of one group were more motivated than the other, one-sided encounters would occur; and if members of both groups were highly motivated to fight for a resource because of its importance, rarity, location, and history of encounters, intense encounters would be most likely. Thus, each type of encounter may represent a grade of intensity according to the relative costs and benefits, to individuals of each group, of defending resources. Cost/benefit decisions are involved and territorial boundaries are flexible according to the demands of the seasonally changing environment.

Comparisons with Other Populations of *C. aethiops*

Comparison of the territorial behaviour of different populations of *C. aethiops* further elucidates the mechanisms and function of territoriality in this species-group. The degree of tolerance or intolerance between groups, the intensity of displays, and the amount of range-overlap varies between populations. On Lolui Island (Uganda: Gartlan and Brain 1968) and at Bokassi (Cameroon: Kavanagh 1981), where the monkeys have very small

ranges in forested habitat, defense of their stable territories is fairly rigid, with little range-overlap. In other areas, such as Kalamaloue (Cameroon: Kavanagh 1981), encounters are more variable and relaxed, and home-range-overlap is more extensive. Areas of range-overlap in Cameroon were 10.3 ha at Kalamaloue (18.2% of the home-range) and 5.8 ha at Buffle Noir (5.6% of the home-range; Kavanagh 1981). The comparable figure for Camp group was 17 ha (9.6% of the home-range). More rigid territoriality may be accompanied by smaller areas of range-overlap, as suggested by Kavanagh's descriptions, but unfortunately no comparative data on frequency of encounters are available from the Cameroon sites. Neither does this take account of seasonal variation in the intensity of territorial interactions, which was clear at Mt. Assirik. Struhsaker (1967a) described seasonal variation in the degree of range-overlap and intensity of encounters at Amboseli (Kenya): as a deviation from the normally rigid territoriality, vervet groups showed considerable mutual tolerance in the vicinity of small water-holes. In contrast, Wrangham (1981) reported that female vervets in one group at Amboseli were prevented from gaining access to a waterhole in a neighbouring group's range, through typical patterns of range defense.

The identity of participants in intergroup encounters varies among populations. Only adult males took part in encounters at Mt. Assirik, except in the rare woodland encounters. A similar pattern seems to occur in Cameroon (Kavanagh 1981). At Amboseli, however, it was common for females to be actively involved in encounters (Cheney 1981). The reason for this difference is unclear. There is an interesting similarity between encounters at Amboseli, where the habitat is very open, and the few encounters in open woodland at Mt. Assirik, which did involve females and young, and occurred on the ground amidst much intergroup 'chutter' calling (Struhsaker 1967a).

Adult males at Amboseli were, however, more aggressive towards other groups than were females or young, and aggression from both males and females was directed more towards opposing males than females or young (Cheney 1981). In addition, dominant male vervet monkeys were more involved in displays, herding, and intergroup aggression. There were also differences in the nature of encounters according to the history of male-transfer between groups: there was more aggression from males at encounters between groups that had exchanged males, but more aggression from females at encounters between groups that had no

common history of male-transfer. The only comparative evidence from Mt. Assirik suggests that such situations may not have arisen, since all males that transferred out of Camp group ($n=3$) during this study did not join neighbouring groups, but travelled further afield. This in itself is an important populational difference, since males must transfer without knowledge of potential new groups. All males who attempted to leave Camp group ($n=5$) returned between 2 and 4 weeks later with severe wounds. One such male was seen alone, back in Camp group's territory, barely able to move due to back or leg injuries – he hid in a cave and was not seen again. Two males returned and remained with the group, and two others left the group for a second time, after their wounds had recovered, and did not return. The incidence of such wounds was not restricted to Mt. Assirik; males leaving groups at Amboseli also received injuries (Cheney, personal communication).

The incidence of intragroup aggression or the herding of females by males of the same group was observed only once during intergroup encounters at Mt. Assirik, but was more common at Amboseli and Buffle Noir (Cheney 1981; Kavanagh 1981, respectively). On a single occasion at Mt. Assirik, during a particularly dispersed yet intense intergroup encounter, an adult male from D group attacked an adult female from his own group, biting her in the neck and chasing her into home territory. It may be significant that this occurred in August, at the beginning of the mating season. Cheney (1981) reports transferred males herding females away from the group's periphery during intergroup encounters, and these males were involved in more copulations during the breeding season. The herding of females may reflect a function of territoriality separate from the protection of food-resources, namely to limit competition between males for access to breeding females.

Cheney (1981) provides the only comparative data on frequency of encounters (Table 4). Intergroup encounters were far more frequent at Amboseli than at Mt. Assirik: for example, compare the number of encounters observed between any pair of groups. However, over 50% of encounters at Amboseli involved vocalizations alone, yet this did not occur at Mt. Assirik. In contrast, virtually all encounters at Mt. Assirik involved aggressive arboreal displays from males, whereas this was much less common at Amboseli. The relative absence of suitable tree canopy at Amboseli may account for this difference. Considering only those encounters at Amboseli that were characterized by displays

Table 4. Comparison of territorial behaviour between two populations of *C. aethiops*

	Mt. Assirik	Amboseli
Number of encounters observed	27 ^a	234 ^b
Rate for one group per all-day-follow	1 per 4 days	(3.7) ^c
% of encounters with herding	4%	20%
% of encounters with displays	92%	38%
% of encounters only vocal	0%	53%
% of encounters with intergrp mixing	0%	4%
Non-AM participation in encounters	Rare	Common, but males more aggressive

^a Involving 4 groups: study group with D = 16, with CMM = 6, with AV = 5

^b Involving 10 groups: study groups A with B = 68, B with C = 51

^c See text

Table 5. Comparison of diet, range, and density between two populations of *C. aethiops*. Data from Harrison (1982, in preparation), Wrangham and Waterman (1981), and Struhsaker (1967b)

	Mt. Assirik	Amboseli
Number of species (not insects and grass) comprising 90% of diet	33	11
Local density (monkeys/km ²)	14.3	104
Mean group size	19.2	24
Home range size (ha)	178	41

and aggression (<10%, i.e. eliminating all vocalization-only encounters), the average rate was one encounter per 3.7 days (Cheney, personal communication), compared with one per 4 days at Mt. Assirik. However, each of Cheney's groups was observed for only 2 h per day.

Several pertinent differences between the ecology of *C. aethiops* at Mt. Assirik and Amboseli are summarized in Table 5. The vegetation at Mt. Assirik is far richer than at Amboseli, in terms of the number and diversity of plant-species, and the density and size of trees (see Harrison 1982, in preparation). The higher rate of territorial encounters seen at Amboseli may reflect this relatively poor habitat, together with the high density of monkeys. Since visual contact between neighbouring groups at Amboseli was made every day, a higher proportion of purely vocal territorial interactions may be expected, since these are less energetically costly than physical displays. In addition,

although specific resources are contested during encounters at Amboseli (Cheney, personal communication), the emphasis of territoriality in this dense population of vervet monkeys may lie on the segregation of groups to reduce competition for mates, perhaps more so than at Mt. Assirik. Even with the relatively rich vegetation at Mt. Assirik, the very low density of monkeys, and the large home-ranges, territoriality among the green monkeys emphasises that in such a highly seasonal environment they too are seasonally food-limited, and must compete for resources. In this comparison, group sizes are similar in both populations, refuting Kavanagh's (1981) conclusion that more territorial populations have smaller groups.

Amongst the savanna baboons, only *Papio ursinus* have been recorded as territorial (Hamilton et al. 1976). Even within this species, aggressive encounters between troops are rare in some populations (e.g., Anderson 1981). Hamilton et al. (1976) describe up- and downstream shifting of ranges, in the Kuiseb River canyon, Namibia, in response to the changing location of waterholes. Sleeping sites were the key resource that caused territorial encounters in another region. The ecological circumstances underlying variability in territorial behaviour thus seem consistent between these populations and the green monkeys at Mt. Assirik.

Economic Defendability

In discussing territoriality by individual birds, Brown (1964) emphasised that diversity in territorial systems depended on the influence of two primary variables, competition and economic defendability. In the examples above, similar types of ecological pressures seemed to be acting on both species of primate, as Mt. Assirik and Kuiseb River, and similar types of territorial responses were shown, marked by seasonal flexibility. In terms of Brown's view, each group was competing for resources in a highly seasonal habitat, in which resources were widely spread and thus not always economically defendable.

Brown also suggested that although competition was essential for the evolution of territoriality, different levels of economic defendability would lead to different territorial responses. Mitani and Rodman (1979) have attempted to quantify economic defendability in an analysis designed for cross-species comparisons of group-size, range-size, and territoriality in primates, but also useful for intraspecific comparisons. To maintain a territory, group members must encounter the perimeter

of their range frequently enough to monitor potential intruders. Based on this proposal, Mitani and Rodman used as an index of defendability (D) the ratio of day-range length to home-range area: the higher the index, the more defendable is the territory. In their sample, all populations with indices of defendability of less than one are non-territorial. All territorial populations have indices of greater than one, although a few with such indices are non-territorial. Thus, a high index permits but does not ensure territoriality.

Given that a relationship between defendability and territoriality exists between species, one may expect that variation in defendability within species will also predict variation in territoriality. Mitani and Rodman cite two examples to support this: non-territorial langurs (*Presbytis entellus*) in northern India have an index $D=0.44$ (Jay 1963 quoted in Mitani and Rodman 1979), while a southern population has an index of $D=1.44$, and is territorial (Yoshida 1967). Comparison between two populations of black and white colobus (*Colobus guereza*) shows a similar relationship (Oates 1977; Dunbar and Dunbar 1974). Although there are no reports of *C. aethiops* being non-territorial, it may be that variations in the degree of territoriality between populations is related to differences in defendability. Indices may be calculated for several populations, but only Cheney (1981) provides comparative data on frequency of intergroup encounters: at Amboseli, the frequency of encounters was high, and $D=1.65$ (calculated from Struhsaker 1967b); at Mt. Assirik the rate of encounters was lower, and $D=1.03$. This meets with prediction, that vervet ranges at Amboseli are small enough to be highly defendable, whereas the large home-ranges of green monkeys at Mt. Assirik are less economically defendable. Qualitative differences in the degree of territoriality in two savanna populations in Cameroon were also associated with the predicted difference in defendability (Buffle Noir, $D=1.8$ – higher levels of territoriality; Kalamaloue, $D=1.4$ – lower levels of territoriality: Kavanagh 1981).

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