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

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Received September 1, 1982 / Accepted October 18, 1982

Summary. Territorial behaviour among green monkeys (*Cercopithecus sabaeus*) 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 defendable.

Introduction

There is evidence for many functions of territory 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 defendability: 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) sabaeus*, 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 synchronic 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 x 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 clumpness’ 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 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 x 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).

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 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,