Colin Chapman
Linda Marie Fedigan

Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E1

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Territoriality in the St Kitts Vervet, *Cercopithecus aethiops*

The fact that the vervet monkey (*Cercopithecus aethiops*) has been described as being territorial in some studies and in some habitats, while not in others, suggests that they exhibit facultative territoriality. The generally accepted model for the explanation of variations in territoriality is an economic one in which animals respond to the necessity of resource defence and the facility with which an area can be defended. A 13-month study of the territorial behaviour and ranging patterns of three groups of vervet monkeys living on St Kitts, West Indies found only mild territoriality expressed during intergroup encounters. The home ranges of the groups were shown to be defendable and food resources were distributed in such a fashion that food was reliably available in specific defendable locations. The fact that all groups had a number of food resources available which were either not heavily exploited, or not used at all, and the fact that the study population increased by over 300% in the last decade, suggest that these vervets were not limited by food availability. The most satisfactory explanation for the low level of territorial defence exhibited by the study population is that the groups were previously associated 10 years ago, when they all were members of a single group that was in the process of fissioning. This study demonstrates that in addition to analysing the functional aspects of territoriality, it is important to understand the historical events leading up to them.

1. Introduction

The concept of territoriality has been defined in many different ways (Davies, 1978) and numerous functional explanations have been suggested for territorial behaviour, however defined (e.g., Carpenter, 1958; Hinde, 1956). Even if we are able to agree upon a common definition (such as the one which was originally suggested by Burt, 1943, for mammals, and is now accepted by many primatologists: territoriality is the defence of an area against encroachment by conspecifics) for some animals we may find no single answer to the question, is this species territorial? The vervet monkey (*Cercopithecus aethiops*) is such a species. Although some primates, such as hylobatids and callitrichids, are unequivocally territorial whatever the environmental context, others, for example the common langur (*Presbytis entellus*) and the olive baboon (*Papio ursinus*), are found to defend space and resources in some studies and in some habitats but not in all (Yoshiba 1968, Hamilton *et al.*, 1976). *Cercopithecus aethiops* has long been used as a prime example of a species exhibiting facultative territoriality in response to differing ecological parameters (e.g., Gartlan & Brain, 1968; Kavanagh, 1981).

Given that vervets are one of the most widely distributed species of African monkey, that they are found in a variety of habitats ranging from semi-desert to swamp, and that they are known for their adaptability and flexibility of behaviour, it is perhaps not surprising that their expression of spatial defence should also be variable. However the extent of variation in the reports of territoriality is still striking, ranging from descriptions of frequent and severe intergroup contact aggression, including wounding (Struhsaker, 1967*b*,*c*; Cheney, 1981) to the other extreme in which groups are reported to sometimes merge without agonism (Kavanagh, 1981). Even for the small island of St Kitts in the Caribbean, on

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which colonizing West African vervet monkeys have made their home for the past 300 years (see McGuire, 1974; Denham 1982*a,b*), the reports on territoriality have been conflicting. Poirier (1972) reported the St Kitts vervet to engage in territorial defence, while McGuire (1974) working with different groups, found no evidence of range defence.

This study describes intergroup encounters and pertinent aspects of range use for three groups of vervet monkeys on St Kitts, West Indies. Our findings are compared with previous studies of both St Kitts and African vervets, and several explanations which have been offered for intraspecific variability in territorial defence are evaluated in the light of this comparison.

2. Methods

Field observations were made on three groups of vervet monkeys between October 1981 and November 1982, with an intensive behavioural ecology study on one of the three groups conducted between May and November 1982. All three groups had adjacent home ranges on a high dry savannah-like hill, known as Sir Timothy Hill and its surrounding flatlands. Each group's range was dominated by a fire-affected shrub community, but all group's ranges included a variety of habitat types including; mangrove swamp, open pasture, stands of sea grape (*Coccoloba uvifera*) and densely vegetated drainage ravines.

During the study, the size and composition of the three groups was determined by enumeration (Fedigan *et al.*, 1984) and home range patterns were obtained from quantitative observations of range use.

The seven-month behavioural ecological study was conducted on the group known as TH3. In order to evaluate the ecology of the group's home range, a system of 100 m by 100 m quadrats was placed over the group's home range, and each quadrat was evaluated on its density and diversity of all plants and just food plants, its level of human disturbance, and the amount of cover it provided the vervets. Since the group used 51 of these quadrats, it was impractical to sample each ecological variable in each quadrat, so a system of 10 m by 10 m plots were randomly placed in each habitat and sampled for each of the ecological variables. The level of each ecological variable for the quadrat was calculated by summing the proportion of each habitat type in the quadrat, multiplied by the habitat's value on each particular ecological variable. Diversity was calculated using the Shannon–Wiener index. Finally, since the area was affected by humans, either directly by people walking through it, or indirectly by areas having previously been cleared for fire wood, each quadrat was qualitatively ranked on the level of human disturbance.

The behaviour of the TH3 group was sampled over the duration of the behavioural ecological study, using a focal animal sampling system which employed a five minute session. In total, 220 hours of focal animal data were collected.

Observations on intergroup encounters were collected opportunistically whenever groups made contact. Since individual identifications of all of the animals in all three groups was not possible, intergroup contact had to be defined by some means other than group membership. Groups were considered to be in contact whenever two groups were clearly seen to approach each other, or when it was possible to obtain a count on an age/sex category which was above that known for any group in the area. In instances where groups did not mix, an intergroup encounter was still considered to have occurred if any of the members of the groups involved were within 30 m of each other and if both groups had clear visual contact with the other.

3. Results

Behaviour during Intergroup Encounters

The members of the three Sir Timothy Hill groups were rarely seen to come into contact (approximately once a month) during the 13 months of our study, and when they did so, the encounters were mild in nature, involving very little agonism. Adult and subadult males performed the only behaviours which appeared to be territorial in nature: vigilance as the two groups came into visual proximity, and branch-shaking displays. Females and young typically continued in the activity in which they were engaged before the encounter took place, and during the intermixture of two groups, non-agonistic behaviours between members of different groups, such as play and sitting in proximity were seen to occur.

Occasionally during intergroup encounters some threat displays and chasing were observed. It was difficult to determine if the agonism was directed at group members or outsiders. In the vervet monkey some intragroup agonism has been reported during encounters between two groups (Cheney, 1981; Kavanagh, 1981; Struhsaker 1967*b*). In particular, adult males have been reported to attempt to herd females of their own group, who then coalesce against them. Herding of females by adult males during intergroup encounters has not been reported on St Kitts. On one occasion a subadult male was seen to leave the main body of one group during an encounter, cross an open area, and join the main body of the second group. He quickly mounted two adult females in succession without interference from other males, who obviously watched the interaction. It is not known to which group the male originally belonged.

Poirier (1972) reported that St Kitts vervets engaged in territorial exchanges in which males gave loud rolling barks, leapt around in the trees in clear view of opponents, and sat in visible elevated positions while exposing their striking white chests. However, McGuire (1974) felt that such behaviours occurred in the context of intra rather than intergroup agonisms. We observed males leaping around in trees and sitting in visible positions in *both* contexts, but did not hear such displaying males give loud rolling barks. Thus the only agonistic behaviours in our study which were clearly observed to occur between groups were branch-shaking displays and "vigilance". Poirier (1972) argued that adult males exposed the strikingly white portion of their chests in a stereotyped sitting posture, as a visual distance-maintaining mechanism. Many studies have described a behaviour performed primarily by primate males in which an individual sits in an elevated and prominent position from which he can both see and be seen (e.g. Hall, 1963; Deag, 1973; Hamilton *et al.*, 1975; Kavanagh, 1981; Harrison, 1983). Although vigilance may function primarily to give a male a clear view of the surrounding area, it seems possible that "vigilance" may function as a signal to other groups as well. The monkeys on St Kitts are very discrete and usually hide behind foliage, because of heavy human predation, and thus it was always striking to see males become prominently visible in the trees shortly before their groups came into proximity. As two groups approached one another the formerly vigilant males would begin to leap rapidly through the trees, with excentuated "splash" landings, and deliberate branch shakings. Typically, other animals would avoid the displaying individual. Branch-shaking displays are another commonly described feature of primate male territorial behaviour (e.g., Cheney, 1981; Hausfater, 1972; Hall & DeVore, 1965; Marler, 1969; Poirier, 1969).

On the other hand, there are a number of commonly described territorial behaviours, typically those involving more intense agonism, which we did not observe in the St Kitts

vervet. For example, no animal was observed to be caught and no physical contact was ever observed to result from the leaping displays. No wounding of any kind was observed to occur when groups were in contact. These mild forms of intergroup encounters on St Kitts are in contrast to the observations made by Struhsaker (1967*a*,*b*) and Cheney (1981) in East Africa. Cheney (1981) reported that 47% of the intergroup encounters involving the vervets of Amboseli National Park, Kenya involved either aggressive chases, hits or bites. Almost all observers report vocalizations to form a prominent part of vervet territorial encounters, although Cheney (1981) found females to be more vocal in this context, while Kavanagh (1981) and Poirier (1972) emphasized the loud territorial bark of males. In contrast, most of the intergroup encounters we observed were noticeably silent. In fact, the general absence of vocalizations in all contexts is one of the more striking features of our study population. Chases between males and even close contact threat displays usually occurred in total silence. Again, since human predation is heavy on the St Kitts vervet and human hunters are known to rely on the sound of the animals, 300 years of selection against vocalizers may have affected this aspect of territorial behaviour (see also Kavanagh 1980 on the silence of crop-raiding vervets in West Africa).

In summary, a few mildly agonistic behaviours which have been interpreted as defence of range in other studies were seen to occur between the three Sir Timothy Hill groups. However these patterns were exclusive to males, and in spite of such displays, groups came into contact and even merged peacefully for up to five hours.

Range Use and Intergroup Encounters

Intraspecific variability in territoriality has often been explained on the basis of differences in demographic and ecological parameters. Thus, in order to demonstrate how environmental factors may have influenced the intergroup encounters in our study population, and to allow comparisons to be effectively made with earlier studies of vervet territoriality, it is important to describe such demographic and ecological patterns as group size, home range size, population density and dispersion, as well as the location of essential resources such as food, water and sleeping sites. The three study groups which utilized the slopes and surrounding flat lands of Sir Timothy Hill had the following age/sex compositions: (1) group TH1, 17 adult males, two to three subadult males, 21 adult females, two subadult females, six to seven juveniles, four infants and four unidentified members; (2) group TH2, 10–11 adult males, four to five subadult males, 19 adult females, three subadult females 13–16 juveniles, and nine infants; (3) group TH3, nine to 10 adult males, two to three subadult males, 18 adult females, two to three subadult females, seven to eight juveniles and 11 infants. The total population averaged 169 over the study period. In comparison with other studies of vervet monkeys in Africa and on St Kitts, this population has relatively large group sizes (TH1 = 54–60; TH2 = 58–63; TH3 50–53) (Table 1, column 3). This corresponds to a relatively high regional population density for the Sir Timothy Hill area of 174·2 individuals per km^2. The size of the home ranges of the study groups were: TH1, 0·14 km^2, TH2, 0·29 km^2 and TH3, 0·54 km^2.

The three study groups differed in the extent to which they overlapped with their neighbours. The TH1 group only overlapped by 0·003 km^3 with all neighbouring groups, which was only 3% of its range size. TH2 shared a total of 31% of its range with the TH1 and TH3 groups. The TH3 group overlapped with a group from further down the penninsula, which was not intensively observed, as well as the TH2 group, subsequently sharing 25% of its range with other groups. In comparison with both Kavanagh's (1981)

Table 1 **Intraspecific variation in vervet territoriality, demography and habitat**

Study	Territoriality	Group size	Range size km²	Population density	% overlap	Index of defendability	Habitat	Location
Hall & Gartlan (1965)	Yes	12·1	—	—	—	—	Mixed	Lolui Island
Gartlan & Brain (1968)	Yes	6–21	—	88·8	—	—	Mixed	Lolui Island
Struhsaker (1967)								
1530	Yes	16·4	0·96	17·1	—	1·17	Savanna	Amboseli
P		17·2	0·19	90·5	—	3·91		
1500		28·3	0·18	157·2	—	—		
CF		49·9	0·34	146 81	—	—		
Poirer (1972)	Yes	20–30	—	—	—	—	—	St Kitts
Baskin & Krige (1973)	Yes	38/19	—	—	—	—	Urban/Bush	Natal, S. Africa
McGuire (1974)	No	4–65	0·16–0·44	—	—	—	Mixed	St Kitts
Dunbar (1974)	Mild	11·8	0·20	59	40	—	Mixed	Senegal
Galat & Galat-Loung (1976)	????	33–47	0·18	239	—	—	Mangrove	Senegal
Cheney								
(1981 *a*)	Yes	23–29	0·4	54·2	—	—	Savanna	Amboseli
(1981 *b*)		10–17						Game Reserve
(1981 *c*)		21–30						Kenya
Kavanagh (1981)								
Bakossi VI	Yes	11	0·12	112·6	0·0	—	Farmland	Cameroon
Bakossi V	Yes	18	0·15	112·6	0·0	—	Farmland	Cameroon
Bufflenoir	Yes	18	1·03	18·0	5·6	1·8	Mixed	Cameroon
Kalamaloue	No	76	0·56	149·0	18·2	1·4	Savanna	Cameroon
Harrison (1983)	Yes	18–28	1·78	14·3	9·6	1·03	Mixed	Senegal
This study								
TH1	Mild	54–60	0·14	407·1	3·0		Savanna	St Kitts
TH2		58–63	0·29	208·6	31·0			
TH3		50–53	0·54	93	25	1·81		

and Harrison's (1983) estimates of range overlap (Table 1, column 6), the average degree of overlap for the St Kitts groups is much higher. The fact that all three groups show similar degrees of territoriality, while the percentages of range-overlap differ considerably, does not lend support to Kavanagh's (1981) suggestion that strong territorial behaviour corresponds to the degree of range overlap.

The intensive study of the behavioural ecology of the TH3 group provided detailed information on the group's ranging pattern, such that the group's core area could be identified. Following Kavanagh (1981) the group's core area was defined as the area encompassed by those 100 m by 100 m quadrats in which the group spent more than 1% of the total observation time. Using this criteria 31% of the group's home range was considered core area. Eighty percent of the intergroup encounters occurred in the core areas, thus demonstrating that the mild nature of territorial encounters was not a consequence of the groups encountering each other only in peripheral areas.

It is possible that the mild nature of the territorial encounters is related to the fact that the groups only use a small proportion of their total range in any one day, thus the probability of encountering an intruder would be small. Mitani & Rodman (1979) argued that territorial defence would only be expressed in those instances where the group's day range is such that it brings them into contact with their boundaries sufficiently frequently to monitor the location of the neighbouring groups. They presented an index of defendability (D) which related day range to range size such that when the index was greater than 1·0 it implied that the study group had frequent contact with its boundaries, conversely a low index implied infrequent contact with it's boundaries. All populations that Mitani & Rodman examined that exhibited territorial defence had a defendability index of 1·0 or greater, however some non-territorial populations did as well. In our study, day range information was collected for the TH3 group only. This group has a defendability index of 1·81, suggesting that it encounters range boundaries sufficiently frequently to make defence of such boundaries feasible. The defendability index for group TH3 is higher than that calculated for other vervet populations which are described as defending territories much more vigorously (Table 1, column 7).

It has commonly been suggested that territorial defence may serve as a means to protect a food source (Brown, 1964; Hamilton *et al.*, 1976; Kavanagh, 1981; Harrison, 1983), In order for such defence to be advantageous to a primate group, the food resource must be both limited and readily defendable. The food and water resources exploited by the TH3 group were quantitatively investigated during the eight-month period when this group was intensively studied. During this period the vervets were observed to feed on 28 different plant species. Evidence from weekly phenological reports on the 11 most frequently utilized plant species suggests that the vervet population had a wide range of food items available to them that were not commonly utilized. For instance when clammy cherry trees (*Cordia obliqua*), the most frequently used plant, (34% of total observed feedings) did not bear fruit, the vervets rapidly began foraging on a number of plant species, seven of which had not been previously utilized.

Wrangham (1981) observed intense competition for water in groups of vervet monkeys in Amboseli National Park, Kenya, which he suggested stressed some individuals to such an extent that they were unable to maintain adequate physical condition. McGuire (1974) suggested that the availability of water might be limiting the vervet monkeys living on the dry peninsula of St Kitts. While there were prolonged periods when the study group did not

have access to standing water, there was no obvious evidence that the study groups were water stressed. A number of the fruits that were a major part of the study group's diet were very succulent and may have in themselves provided an adequate supply of water. In periods of time when there were only a couple of areas which contained standing water, the vervets did not appear to associate in these areas more than when the water was not available. Also, no direct conflict was observed over access to the standing water. This evidence would suggest that the vervets of the study group were not limited by their access to water, and also that they were not selecting areas, based upon the availability of standing water.

Harrison (1983) suggested that the territorial boundaries of the vervets he studied in Senegal were resource dependent, and he demonstrated how the areas of overlap and contest were often unique in containing some valuable resource. To evaluate the ecological nature of the overlap areas, the 100 m by 100 m quadrats which the TH3 group shared with its neighbouring groups were compared to the non-overlapping quadrats. None of the 12 variables examined exhibited significantly different levels when overlapping and non-overlapping quadrats were compared. The size classes of plants did not differ in terms of density (high: $t = 1{\cdot}23$, $P = 0{\cdot}234$; medium: $t = 0{\cdot}89$, $P = 0{\cdot}381$; low: $t = 0{\cdot}96$, $P = 0{\cdot}345$) or diversity (high: $t = 0{\cdot}02$, $P = 0{\cdot}988$; medium: $t = 1{\cdot}31$, $P = 0{\cdot}205$; low: $t = 1{\cdot}28$, $P = 0{\cdot}223$). Nor did any of the size classes of food plants differ between overlapping and non-overlapping quadrats in terms of density (high: $t = -0{\cdot}02$, $P = 0{\cdot}987$; medium: $t = -0{\cdot}54$, $P = 0{\cdot}599$; low: $t = -0{\cdot}38$, $P = 0{\cdot}707$), nor diversity (high: $t = 0{\cdot}55$, $P = 0{\cdot}585$; medium: $t = -1{\cdot}03$, $P = 0{\cdot}313$; low: $t = 1{\cdot}84$, $P = 0{\cdot}80$). Neither type of quadrat differ significantly in terms of the amount of cover it provided ($t = -1{\cdot}51$, $P = 0{\cdot}146$), or in the assessed amount of human disturbance ($t = 1{\cdot}84$, $P = 0{\cdot}077$).

4. Discussion

Several explanations have been offered for interspecific variability in spatial defence, and we will examine these in turn. It is most commonly advanced that territoriality will exist whenever the benefit from defending an area is greater than the expense (Brown, 1964). If this economic view of territoriality is true for the population studied on St Kitts, it should be possible to argue that either the areas which the groups occupy are not worth defending, or that they are too expensive to defend.

Home ranges are differentially defendable, that is not all ranges offer equal possibility for spatial defence. Boundary defence is related to the ability of a group to detect intrusion (Mitani & Rodman, 1976; Hamilton *et al.*, 1976; Harrison, 1983) which in turn is related to the group's home range size, daily ranging pattern and food availability. Hamilton *et al.* (1976) found that one group of baboons which they studied was generally within hearing distance of its boundaries and encountered all of its boundaries once throughout the day, this group defended well-defined boundaries, whereas a group which had a longer home range only defended its boundaries near a waterhole. The home range sizes of the vervet groups we studied were all smaller in size than that of a number of groups reported to have vigorous spatial defence (Table 1, column 4), suggesting that the group's home range sizes did not limit their ability to defend their borders. Kavanagh (1981) suggested that the reliability of specific locations to provide food would favour spatial defence. The TH3 study group had very specific foraging locations which were largely constant over the duration of the study. Thirty-five percent of the foraging performed by the group occurred in only 6%

of the group's home range. This would definitely indicate that this group had very localized food resources that it could have defended. The degree of range overlap influences the probability of encountering invading groups and affects the defendability of a home range. When the Sir Timothy Hill groups trespassed on one another, they tended to do so to such an extent that they entered into the core area of the other groups. Thus, when intrusion occurred it was likely that it would be detected. It is reasonable to conclude that the Sir Timothy Hill groups are easily capable of defending their home ranges from intrusion.

Variation in the intensity of vervet territorial defence has also been related to variation in necessity for defence (Kavanagh, 1981; Harrison, 1983). The reasons why it is not always necessary, or economical to defend an area have been suggested to depend on population density, the availability of resources and the nature and intensity of predation. Yoshiba (1968) found that langur (*Presbytis entellus*) groups with high population densities actively defended areas while groups with low population densities did not. Hamilton *et al.* (1976) found a similar trend with baboons. If population density had a direct affect upon whether or not a group exhibited spatial defence, it would be expected that the mild nature of territorial defence in the St Kitts groups would be related to low population densities. This is not the case, the actual group densities are at the upper end of those reported for *Cercopithecus aethiops* to date (Table 1, column 5).

If a group of primates is food limited and the food is dispersed in a predictable fashion in space and time, it is hypothesized to be advantageous for the groups to maintain exclusive use of the resources in the area (see Kavanagh, 1981 and Harrison, 1983 for vervets, and Hamilton *et al.*, 1976 for baboons). There is little evidence to suggest that the groups studied on St Kitts were food limited. If one favoured plant type was no longer abundant, the groups always had a number of secondary resources to fall back on. All groups had a variety of food resources available to them which were simply not exploited. The best example of this is the fact that these vervets did not utilize either the abundant land and sea crabs nor the mangroves, both of which Galat & Galat-Luong (1976) report were heavily exploited by the groups they studied in Senegal. In St Kitts, the group which was intensively studied (TH3) was found not to preferentially select areas of high food plant density, suggesting these areas were not heavily exploited by the group, as would have been expected if the group were limited by food (Chapman, 1983). This group also spent only 28% of its day engaged in foraging. It might be expected that a food limited group would spend a major portion of its day foraging. The final evidence which suggests that the groups are not presently food limited is that the population of Sir Timothy Hill increased from 50 to 176 individuals over the last decade. This evidence would indicate that the study population was not food limited, and that it was not necessary to defend territories in order to restrict access to scarce food resources.

In sum, most of the evidence, as based on traditional explanations for spatial defence, would indicate that our study groups of St Kitts vervets *should* be territorial. That is, they have home ranges and food resources that can be easily defended, their favoured foods are localized and predictable, and the population density is relatively high. On the other hand, the available evidence indicating that these groups are not food-limited would suggest that it is not necessary for them to defend their food resources, and would lead us to expect the low levels of territoriality which we did indeed observe.

A possibly more satisfactory explanation for the low level of territorial defence found in our study population and one that circumvents the difficulty of cost-benefit analyses,

concerns the historical relationships of the groups involved. In 1972, McGuire (1974) conducted a study of the monkeys in the same area, at the beginning of which all of the vervets on Sir Timothy Hill formed a single group composed of three subgroups. All of these subgroups shared a single sleeping area, and socialized together in the early morning and late afternoon, but they maintained distinct daytime ranges. This description suggests that the one large group was in the process of fissioning into three independent smaller groups, and it seems likely that the three subgroups which McGuire described became the three groups observed in our study. If this is the case, it is possible that the prior associations between the groups involved may explain the mild nature of the territorial encounters. In comparing the present description of encounters between these groups with those described by McGuire (1974), it is apparent that there is more tension associated with encounters today, than 10 years ago. This suggests that as prior associations between the monkeys weaken, the groups are gradually becoming more territorial.

Both Hamilton *et al.* (1976) and Cheney (1981) have argued that long term associations between groups and individuals may influence the manner in which spatial defence is conducted. The findings of this study also indicate that prior relationships may affect the nature and extent of territoriality. Thus we would suggest that in addition to examining the functional aspects of observed intergroup encounters, it is also important to understand the historical events leading up to them.

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