

Ecological consequences of a group fission event in the Tana River mangabey (*Cercocebus galeritus*)

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Abstract

A group of Tana River mangabeys *Cercocebus galeritus* studied in 2000–2001 fissioned into two daughter groups in 2004, the first reported case of fission in *Cercocebus*. Data were collected on each daughter group in 2005–2006 to investigate how the groups divided the parent group's range, the quality of habitat used by each group, and if fruit abundance was correlated with the spatial relationships between the groups. Six days of ranging data were collected each month and input into ArcView GIS 3.3 to measure home ranges and core areas. Phenological data were collected from nine important food species. Habitat quality was measured by counting all reproductive-sized individuals of those nine food species in the ranges. The daughter groups shared the parent group's home range and core area, although the larger group used more of those areas than the smaller group. The two groups got equal quality home ranges and core areas as measured by per capita food trees, but the larger group had access to a larger and richer exclusive area. Proximity of the groups to each other was not correlated with fruit abundance. This study contributes to the small body of literature that addresses ecological consequences of primate group fission.

Key words: *Cercocebus galeritus*, group fission, habitat quality, Kenya, primate, ranging

Résumé

Un groupe de cercocèbes de Tana *Cercocebus galeritus* étudié en 2000–2001 s'est scindé en deux groupes en 2004, le premier cas de scission rapporté chez cette espèce. Des données furent récoltées pour chaque nouveau groupe en 2005–2006 pour étudier comment ils s'étaient partagé l'aire de distribution du groupe d'origine et la qualité de l'habitat fréquenté par chacun et pour voir si l'abondance

de fruits était liée aux relations spatiales entre les deux groupes. Chaque mois, les données sur la distribution étaient collectées pendant six jours et elles étaient introduites dans ArcView GIS 3.3 pour mesurer les aires de distribution et les zones centrales. On a aussi collecté des données phénologiques pour neuf espèces alimentaires importantes. La qualité de l'habitat fut mesurée en comptant tous les individus de ces neuf espèces en âge de se reproduire et qui se trouvaient dans l'aire de distribution. Les nouveaux groupes partageaient l'aire de distribution et la zone centrale du groupe initial, mais le plus grand des deux fréquentait une plus grande partie de ces zones que le plus petit. Les deux groupes avaient des aires de distribution et des zones centrales de qualité égale si on les mesure selon le nombre d'arbres alimentaires par tête, mais le plus grand groupe pouvait accéder à une zone exclusive plus grande et plus riche. La proximité des deux groupes n'était pas liée à l'abondance de fruits. Cette étude vient contribuer au peu de littérature existante traitant des conséquences écologiques de la scission d'un groupe de primates.

Introduction

Permanent group fission (i.e. not temporary subgrouping displayed by fission-fusion societies) has been observed in a variety of primates: lemurs (Jolly *et al.*, 2002; Bayart & Simmen, 2005; Erhart & Overdorff, 2008), howlers (Miranda *et al.*, 2006), colobines (Hohmann, 1989), cercopithecines (Henzi, Lycett & Piper, 1997; Janmaat & Chancellor, 2010) and apes (Nsubuga *et al.*, 2008). Primate groups fission when reproductive success decreases (Hohmann, 1989; Jolly *et al.*, 2002; Nsubuga *et al.*, 2008), when individuals can no longer maintain group social cohesion (Malik, Seth & Southwick, 1985;

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Henzi, Lycett & Piper, 1997; Miranda *et al.*, 2006), and when intragroup feeding competition is too high (Dittus, 1988; Erhart & Overdorff, 2008).

Although many studies have investigated social consequences of group fission, few have looked at ecological consequences. One ecological consequence is a change in home range size and location. One daughter group may completely leave the original range, the daughter groups may divide the original range with no overlap, or the daughter groups may share the original range (Struhsaker & Leland, 1988; Jolly & Pride, 1999). In addition, one or both groups may increase their range. Sharing the original range is the most common response when groups fission (Cords & Rowell, 1986; Struhsaker & Leland, 1988; Ménard & Vallet, 1993; Okamoto & Matsumura, 2001; Windfelder & Lwanga, 2002). Sharing the original range may serve to reduce costs involved with a larger group, without the added risks of expanding into new habitat. One potential risk of expanding into new habitat is an increase in aggressive encounters with groups already established in those areas (Struhsaker & Leland, 1988; Jolly & Pride, 1999). Another risk is an increase in predation because of the unfamiliarity of the new area (Isbell, Cheney & Seyfarth, 1990). Finally, ranging through new, unfamiliar habitat may decrease foraging efficiency. This is because groups moving through new areas often increase their daily distance (Windfelder & Lwanga, 2002; Janmaat & Chancellor, 2010), which is energetically costly. Individuals may also not be as efficient in finding ephemeral fruit sources (Janmaat & Chancellor, 2010).

Another potential ecological consequence of group fission is a change in habitat quality (e.g. food species density, tree density) of the resulting home ranges. When the daughter groups are of unequal size, the smaller group is often subordinate (Malik, Seth & Southwick, 1985; Cords & Rowell, 1986; Bayart & Simmen, 2005) and has a poorer quality habitat. The smaller of two daughter groups of blue monkeys *Cercopithecus mitis stuhlmanni* got fewer of the frequently used quadrats of the original range and did not get exclusive use to any of them (Cords & Rowell, 1986). The smaller group also got a lower quality habitat as measured by tree species density, stem density, mean height and number of fruiting trees.

Here, I present the first observed case of group fission in a *Cercocebus mangabey*, the Tana River mangabey (*C. galeritus*, Peters, 1879) and an investigation of the ecological consequences of this fission. I examined the daughter groups' home ranges; I measured the location of the groups' ranges in relation to the parent group's range,

the amount of range overlap and the distance between groups during simultaneous follows. I hypothesized that the daughter groups will share the original range.

I examined the quality of the daughter groups' home ranges, core areas and the areas which each group used exclusively. Tana River mangabey abundance per forest is correlated with basal area of their top 15 food species (Wieczkowski, 2004). I therefore used density of important food trees as a measure of habitat quality. Wieczkowski (2005) found that two mangabey groups had access to the same number of trees per mangabey (271 and 320), regardless of extremely different group size (50 and 17) and home range (46.75 and 18.75 ha). I therefore also used per capita number of trees to compare habitat quality. As the daughter groups were of unequal size, I hypothesized that the large group would have a higher quality home range, core area and exclusive area.

Finally, I investigated if feeding competition influences the daughter groups' reactions to each other. Kinnaird (1992) found that two mangabey groups that she simultaneously followed avoided each other when fruit abundance was low and either fought or merged when fruit abundance was high. I hypothesized that distance apart will be negatively correlated with fruit abundance, as measured with phenological data. I also hypothesized that range and core area overlap will be positively correlated with fruit abundance.

Material and Methods

Study area and study groups

The Tana River mangabey (*Cercocebus galeritus*) is endemic to a 60-km stretch of the lower Tana River in Kenya (1° 40'–2° 15' South, 40° 05'–40° 10' East; Fig. 1). The species is endangered (IUCN, 2012). The area is semiarid, with mean annual precipitation less than 500 mm, and mean daytime temperatures of 30–38°C. The riverine forest patches are dependent on the river's natural flooding regime and height of the groundwater table (Hughes, 1988).

The Mchelelo West mangabey group has been the subject of three long-term studies. The group was 36 individuals in 1974 (Homewood, 1976), then declined to seventeen individuals in 1988–1989 (Kinnaird, 1990), but increased to 50 individuals during the observation period of 2000–2001 (Wieczkowski, 2005). On the basis of observations by a colleague (David N.M. Mbora, pers. obs.) from July through September 2004, the Mchelelo West

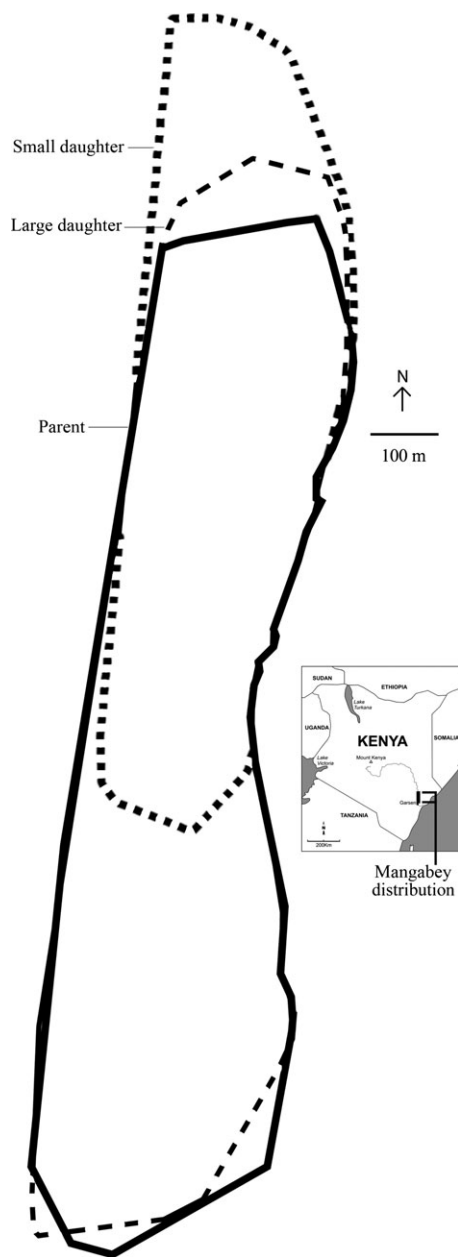


Fig 1 Home ranges (minimum-convex polygon) of the three groups. The parent group's range is a solid line, the large daughter group's range is a dashed line, and the small daughter group's range is a dotted line. The inset map shows the location of the Tana River mangabey's distribution along the lower Tana River

group had fissioned into two groups that were spatially separate. Recognition of the groups as daughter groups was based on level of habituation, location and total

number of individuals. The parent group fissioned unevenly; the large group had 48 individuals, while the small group had 29 individuals.

Ranging behaviour

Data were collected on the parent group from August 2000 until July 2001 and on the daughter groups from July 2005 until June 2006. Each group was followed from 07:00 to 18:15 hours for three consecutive days twice per month (except in November 2000, December 2000, January 2001 and July 2001 when the parent group was followed for only three days). During the second follow each month in 2005–2006, the daughter groups were followed simultaneously with the help of field assistants. Every half-hour, five minutes were spent marking the location of each individual on maps. I superimposed a 50 m × 50 m grid over the maps and noted the 0.25 hectare quadrats that had at least one individual. All quadrats entered for the full year were used to calculate habitat quality (see below) of the home range; the quadrats responsible for 50% of the group's sightings (in descending order) were used to calculate habitat quality of the core area. For each five-minute mapping sample, the group's centre of mass was determined as the centre of a polygon drawn around all sighted animals (Waser & Floody, 1974). The centres of mass were manually input into ArcView GIS 3.3 with the Animal Movement Extension to calculate home ranges and core areas.

Monthly home range sizes were calculated for both daughter groups using the minimum-convex polygon (MCP; Mohr, 1947) and 95% fixed kernel (Worton, 1989) methods, and monthly core area sizes using the 50% fixed kernel method (Worton, 1989). Annual range sizes were calculated for all three groups using the same methods. The MCP method draws a convex polygon around the outermost locational records and calculates the area of the resulting shape. This common method is easy to use. However, it overestimates range area by including areas never used and does not provide information on the intensity of range use (Worton, 1987). In addition, estimates are highly correlated with the number of data points; it is estimated that with fewer than 25 points, the range estimate is half of the true size (Schoener, 1981). Daily range estimates ($n = 23$), therefore, were not calculated using MCP. The kernel method uses a more accurate probabilistic model involving the likelihood of finding an individual at a particular location (Worton,

1989). It also provides information on the intensity of range use. The mangabeys do not cross the river; their ranges are bordered on the east by the Tana River. I used the X-Tools Extension to remove the river area from all range estimates.

When the daughter groups were followed simultaneously, I calculated range and core area overlap in hectares and as a percentage. The percentage of overlap was calculated by dividing the number of hectares the groups shared by the total number each group used. I used a two-tailed Wilcoxon signed-ranks test to determine if percent overlap differed between the two groups. I also measured the distance between each group's centre of mass every half-hour and calculated a mean distance apart for each day or 3-day follow.

Fruit availability

Nine palm, sub-canopy tree and canopy tree species were monitored for phenological activity between July 2005 and June 2006. These species were the top palm, sub-canopy tree and canopy tree species contributing to the annual diet of the parent group (Wieczkowski, unpublished data). These species accounted for 87.3% of the large group's and 89.3% of the small group's annual plant diet (78.7% and 82.7% of complete annual diet respectively) (Wieczkowski, unpublished data). Fifteen trees of each species were randomly selected throughout the study area and monitored monthly immediately prior to and/or subsequent to the first mangabey follow. The presence of fruit (unripe, ripe) in the canopy was scored on a 0–5 scale measuring the proportion of the total canopy covered (0 = 0%, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%). Each tree's diameter at breast height (DBH, measured at 1.5 metres above the ground (Brower, Zar & von Ende, 1998)) was measured, and a mean for each species was calculated. Each mean monthly fruit score was multiplied by the species-specific mean DBH and density values (see below) to arrive at a biomass score. This biomass score better estimates available fruit per hectare (Chapman *et al.*, 1992; Chapman, Wrangham & Chapman, 1994).

Habitat quality

The study area has clearly marked quadrats of 0.25 ha. Within each quadrat, I enumerated all reproductive-sized individuals of the species included in the phenological

sample and converted to density (trees per ha). I measured habitat quality by calculating an overall density for those quadrats included in each group's home range, core area and exclusive area. I compared habitat quality with two-tailed Kruskal–Wallis tests and pairwise Mann–Whitney tests if necessary. I also measured habitat quality by calculating a per capita density (trees per mangabey) by dividing the overall tree number by the number of mangabeys in the group. I compared per capita habitat quality with two-tailed Friedman tests and pairwise Wilcoxon signed-ranks tests.

Results

How the group split the home range

Using MCP (Fig. 1), home range was 46.3 hectares for the parent group ($N = 1398$ mapping samples), 47.4 ha for the large group ($N = 1610$) and 31.5 ha for the small group ($N = 1610$). Using 95% fixed kernel method (Fig. 2), home range was 52.2 ha for the parent group, 41.2 ha for the large group, and 26.4 ha for the small group. The large group included 3.6 ha in the south not used by the parent group, while the group did not use 14.6 ha to the north and west. The small group used 4.2 ha not used by the parent group, expanding to the north, and did not use 29.7 ha to the west and south. Core areas (Fig. 3) were 17.6 ha for the parent group, 9 ha for the large group and 6.5 ha for the small group. The large group's core area was almost entirely within the parent group's core area; only 0.2 ha were outside. Less than half of the small group's core area (2.7 ha) was in the same location as the parent group's.

On an annual basis, the overlap between the daughter groups' home ranges was 25.6 ha (MCP), 19.4 ha (95% fixed kernel) and 1.5 ha (core area) (Table 1). In four months, the two groups did not overlap in any of the range measurements. In three months, they overlapped in their home range, but not in the core area. When monthly overlap is measured as a percentage, the small group shared more of its range with the large group when measured with the MCP ($Z = -2.028$; $P = 0.043$), but the other measurements did not reach significance (95% fixed kernel: $Z = -1.820$; $P = 0.069$; 50% fixed kernel: $Z = -1.483$; $P = 0.138$). Of 34 days of simultaneous follows, there was no overlap in home range on nineteen days (56%) and no overlap in the core area on 24 days (71%).

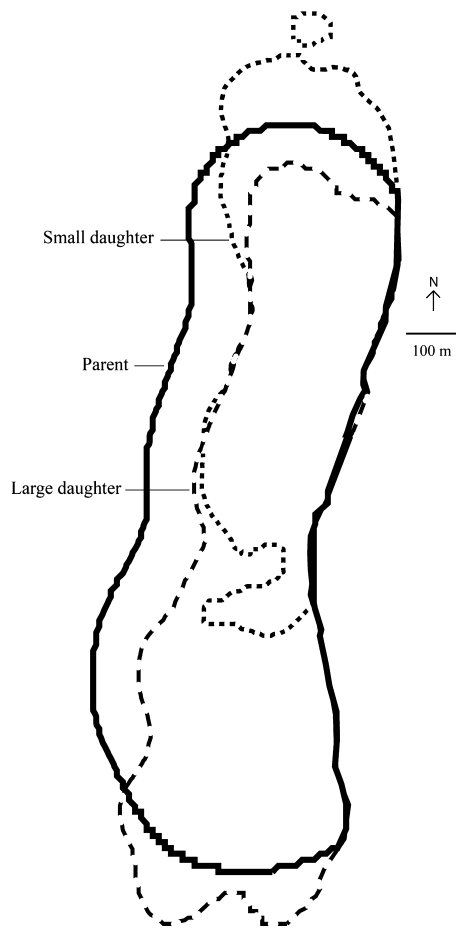


Fig 2 Home ranges (95% fixed kernel) of the three groups. The parent group's range is a solid line, the large daughter group's range is a dashed line, and the small daughter group's range is a dotted line

The minimum distance between the two groups in any single mapping sample was 34 metres in October, whereas the maximum was 1509 metres in July. The mean distance between the groups varied from 489 metres ($N = 69$; $SD = 220.7$) in September to 1001 metres ($N = 69$; $SD = 144.1$) in March.

Habitat quality

The large group's home range had significantly more trees per hectare (436 trees per ha) than the small group's (376 trees per ha) ($Z = -2.474$; $P = 0.13$). Neither the large group ($Z = -0.548$; $P = 0.584$) nor the small group ($Z = -1.720$; $P = 0.085$) had more trees per hectare than

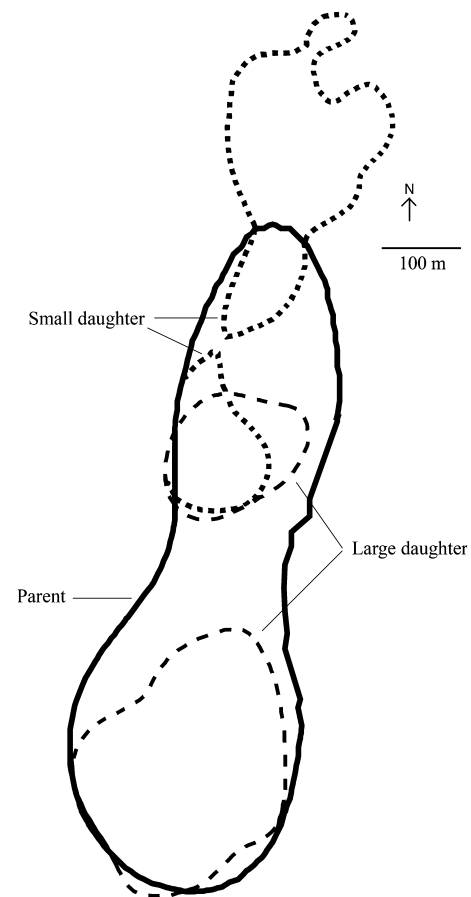


Fig 3 Core areas (50% fixed kernel) of the three groups. The parent group's range is a solid line, the large daughter group's range is a dashed line, and the small daughter group's range is a dotted line

the parent group (416 trees per ha). There was little difference in the number of trees per capita (large group: 452 trees per mangabey; small group: 437 trees per mangabey; $Z = -0.296$; $P = 0.767$). The large group had a higher per capita density than the parent group (356 trees per mangabey; $Z = -2.429$; $P = 0.015$), while the daughter group and the parent group did not differ ($Z = -0.652$; $P = 0.515$).

The large group also had significantly more trees per hectare (524 trees per ha) in its core area than the small group (398 trees per ha) ($Z = -2.410$; $P = 0.016$). Neither the large group ($Z = -1.902$; $P = 0.057$) nor the small group ($Z = -0.421$; $P = 0.674$) had more trees per hectare than the parent group (427 trees per ha). The core areas were essentially equal when the number of trees per

Table 1 Overlap between the two daughter groups in home range and core area in hectares and per cents

	Home range (MCP)			Home range (95% fixed kernel)			Core area (50% fixed kernel)		
	Hectares	Large group – per cent	Small group – per cent	Hectares	Large group – per cent	Small group – per cent	Hectares	Large group – per cent	Small group – per cent
July 2005	0	0	0	0	0	0	0	0	0
August	0.2	1.3	1.5	2.7	13.6	13.9	0	0	0
September	8.4	44.1	56.2	15.4	50.5	72.4	1.2	12.1	24.9
October	8.5	35.9	69.3	14.6	41.4	85	0	0	0
November	14.8	47.8	85.6	24.1	50.8	90.7	3.2	16.8	46.3
December	16.0	49.2	93	26.8	48.9	98.1	3.2	21.3	31.4
January 2006	0	0	0	0	0	0	0	0	0
February	0	0	0	0	0	0	0	0	0
March	0	0	0	0	0	0	0	0	0
April	2.3	16.8	14.3	6	29.3	27.2	1.3	39.1	36.4
May	0	0	0	0.3	1.9	1.3	0	0	0
June	17.6	71.1	76.4	25.7	59.5	72.3	6.9	46.4	46.5
Annual	25.6	54.0	81.3	19.4	47.1	73.5	1.5	37.5	23.1

MCP = minimum-convex polygon.

capita was compared (large group: 106 trees per mangabey; small group: 110 trees per mangabey; parent group: 79 trees per mangabey; $\chi^2 = 5.556$; $P = 0.062$).

The large group had exclusive use of 19.75 ha, while the small group had exclusive use of only 4 ha. The large group's exclusive area had 537 food trees per hectare, significantly more than the 421 trees in the small group's exclusive area ($Z = -2.123$; $P = 0.034$). The large group had significantly more trees per capita (221 trees per mangabey) than the small group (58 trees per mangabey) in their exclusive area ($Z = -2.429$; $P = 0.015$).

Daughter groups' reactions to each other

There were no significant correlations between monthly fruit availability and mean distance the groups were from each other (two-tailed Spearman's correlation; $\rho = -0.438$; $P = 0.155$), overlap in MCP home range ($\rho = 0.036$; $P = 0.911$), overlap in 95% fixed kernel home range ($\rho = -0.036$; $P = 0.913$), or overlap in core area ($\rho = -0.238$; $P = 0.456$).

Discussion

This study presents results from the first permanent group fission observed in a *Cercocebus* mangabey. Three other

Cercocebus species have been the subject of long-term observation: the Sanje mangabey *C. sanjei*, the sooty mangabey *C. atys* and the agile mangabey *C. agilis*. *C. sanjei* is found in groups of 35–60 (Rovero *et al.*, 2009), similar in size to the Tana River mangabey. *C. atys* in Tai, Ivory Coast are found in larger groups, typically numbering 100 individuals (Mcgraw & Zuberbühler, 2007). Group size in *C. agilis* is variable throughout the species, with groups of 7–18 in Gabon (Quris, 1976), 21–22 in Mondika, Central African Republic and Republic of Congo (Shah, 2003), and 134 in Bai Hokou, Central African Republic (Devreese, 2010). The Tana River mangabey group was likely close to 70 individuals when it fissioned in 2004, estimated from the sizes of the resulting daughter groups which together numbered 77 individuals in 2005. A group of 70 is double the average group size of 37 individuals ($n = 41$ groups; Wiczowski *et al.*, 2002).

The lack of the predicted relationship between fruit abundance and spatial relationships (Kinnaird, 1992) could be due to a number of reasons. Perhaps, the groups came closer together to feed on what was available each month; many of the mangabey top food species are found at low density and are clumped (Kinnaird, 1990). Perhaps, the desire to maintain social relationships (Jolly *et al.*, 1993) or the need to establish new range boundaries (Cords & Rowell, 1986; Struhsaker & Leland, 1988;

Okamoto & Matsumura, 2001) brought the groups closer together. On the other hand, perhaps the lower percentages of range overlap in the daughter groups compared with Kinnaird's (1992) study group, whose range was almost completely overlapped, influenced the lack of relationship.

The daughter groups shared the parent group's range, the most common response to group fission (Cords & Rowell, 1986; Struhsaker & Leland, 1988; Ménard & Vallet, 1993; Okamoto & Matsumura, 2001; Windfelder & Lwanga, 2002). Although they ranged annually over the same area, they did not overlap on the majority of days and in four months. This annual overlap, but with time-sharing on a daily or monthly basis, would serve to reduce direct feeding competition (Struhsaker & Leland, 1988). It would also remove the risks of expanding into new habitat, such as encounters with established groups (Struhsaker & Leland, 1988; Jolly & Pride, 1999), predation (Isbell, Cheney & Seyfarth, 1990), and a reduction in foraging efficiency (Windfelder & Lwanga, 2002; Janmaat & Chancellor, 2010). It is not possible to conclude how typical the amount of range overlap between these two groups is for the Tana River mangabey; a group studied by Waser & Homewood (1979) had a range that was overlapped by 36%, while Kinnaird's (1992) group was overlapped almost completely.

The Mchelelo West parent group fissioned into unequal daughter groups, similar to other groups (Malik, Seth & Southwick, 1985; Cords & Rowell, 1986; Struhsaker & Leland, 1988; Windfelder & Lwanga, 2002). The large group did keep more of the original home range and core area, although they expanded almost as much as the small group. The large group did also have a larger and more dense (in terms of food trees per capita) area that was used exclusively by them. However, the number of food trees per capita was equal between the groups' home ranges and core areas.

This study contributes to the small body of literature that addresses the ecological consequences of group fission in primates. Although the reason for the Tana River mangabey's group fission was not investigated, it is important to note the daughter groups shared the parent group's home range and each got an equal quality home range and core area. Because of the good quality of habitat in the Mchelelo West forest complex, the groups were able to do this. This information may be of use to conservation managers in Tana River.

Acknowledgements

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