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ECOLOGY OF THE LOWER TANA RIVER FLOOD PLAIN (KENYA)

By

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INTRODUCTION

The Tana River is the longest river in Kenya. From its sources on Mt. Kenya and the Aberdares to its present mouth at Kipini on the Indian Ocean is a straight distance of 480 km and 800 km following the major directional curves. But a measurement along the numerous meanders of the lower course would yield a length at least double this (see Fig. 1).

In its upper course the Tana flows north, but soon turns south by south-east, which is its direction until it reaches the sea. The limit of the Upper Tana is taken as the Hargazo Falls, which are situated at about the point where the river turns south. It is this part of the river which receives all the tributaries, the last to enter the river being the MacKenzie, which joins it 58 km above the Falls. Only during high flood years does water from other rivers, such as the Tiva, enter the Tana. Thus the river gains no new water in its middle and lower courses, but loses water continuously through evaporation.

In its lower reaches the Tana flows through a broad flood plain. The entire area is covered by recent alluvial sediments brought down and deposited during the annual floods of the river. The flood plain is primarily grass-covered but there are numerous patches of forest and woodland that are apparently edaphic in origin, depending either on the flooding or on the high water table in the flood plain or both.

The forests of the Lower Tana River are the home of two endemic subspecies of primate: the Tana River Red Colobus (*Colobus badius rufomitratus*) and the Tana River Mangabey (*Cercocebus galeritus galeritus*). These are both listed in the *Red Data Book* as endangered. Almost nothing has been recorded of their distribution, status, ecology, and behaviour. The primary purpose of this investigation was to study their distribution

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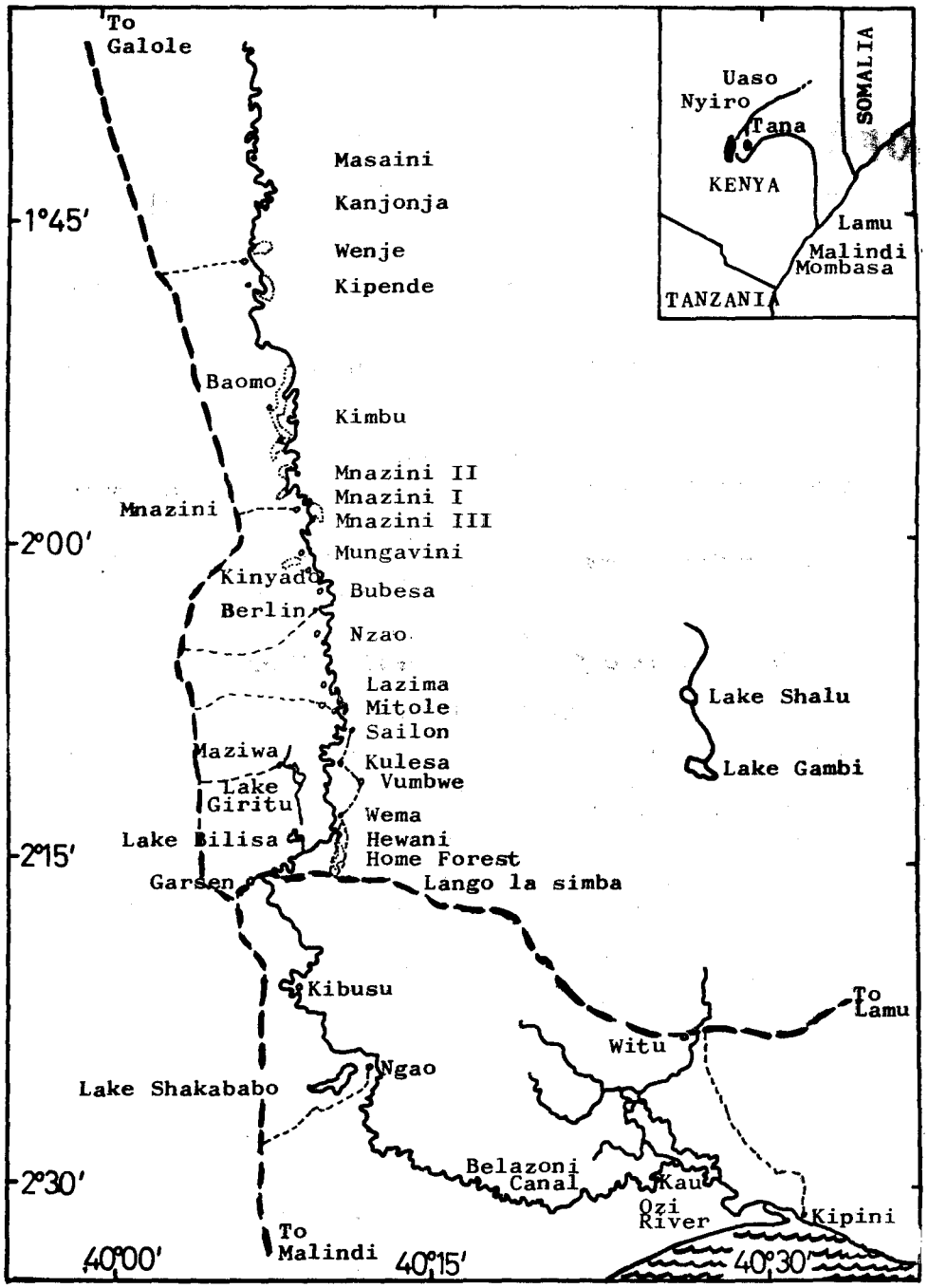

Fig. 1. The Lower Tana River, showing the northern forests of the 1972 expedition. Heavy dotted lines are roads; smaller dotted lines are tracks.

and status with reference to the ecology and fauna of the region. The closest relatives of both monkeys are to be found in the Central African forests, posing striking zoogeographical problems. The ecological survey was therefore undertaken from a problem orientation, as well as a purely descriptive one.

This survey took place in July and August 1972. The feasibility of such a survey was investigated by preliminary visits in 1971 and 1972. We saw colobus in one forest in August 1971, and both colobus and mangabeys in three different forests in February 1972. T. T. Struhsaker visited the area in November 1971, finding mangabeys and colobus in one forest and mangabeys in another. The present survey owes a lot to his encouragement. These initial investigations confirmed that the animals could be found if searched for and that the area was not totally uninhabitable by a scientific team.

METHODS

The authors set up a camp on the Tana River, near Hewani (approximately 02°15'S, 40°10'E). The camp was near a large forest, hereafter called the "Home Forest", along a former river course (see Fig. 2). Almost daily visits were made into this and the nearby Hewani forests, mostly in the early morning and towards evening. Several day-long visits were made to localities upriver. Members of the expedition also made three longer safaris (see Fig. 1):

1. on the right bank as far up as Garissa, crossing the river and going down the left bank as far as Bura;
2. on the right bank to Mnazini and Baomo;
3. and on the right bank downriver to Ngao.

Data on birds and large mammals, including colobus and mangabey, were collected primarily from observations of C. P. Groves. Mistnets were also set up within the Home Forest, and birds caught in them were identified by J. F. M. Horne and measured, then released (a few, however, were collected). Small mammals were trapped by P. Andrews and J. Kinyanjui, mostly in live-traps (wooden live-traps measuring 7 × 8 × 15 cm were used, supplemented on occasion by break-back traps of three different sizes), and either collected or released. Trapping was done for two months in July-August in the Home Forest, Hewani IV and Mnazini I (see Fig. 2). A number of soil pits were dug, under the direction of P. Andrews, and soil samples from them were analysed by the National Agricultural Laboratories, Nairobi. The vegetation was recorded by P. Andrews, and we had the benefit of the five day visit from J. B. Gillett and S. Kibua of the East African Herbarium. The small mammals collected were identified with the help of I. S. Aggundey, and the birds with the help of A. Forbes-Watson, both of the National Museums of Kenya.

We had the assistance of J. Kinyanjui of the National Museum throughout our two month encampment, and from time to time of visitors who stayed for periods of a week to nearly a month.

THE ENVIRONMENT

The Tana River

The lowest part of the Tana River (the delta region below Ngao) is some 30-40 metres wide; further up, it averages 60 m and may reach 100 m in a few places. The river's depth in the dry season is only a few centimetres except for a narrow deep channel. Unlike many rivers, its breadth does not noticeably lessen in the dry season, but the river always occupies its whole bed which is dotted with sandbanks. The bed is raised and kept in place by a natural levee which is breached in places by natural floodwater channels. The height of the banks above the dry season water level is only 1 metre or so in the delta region, but up to 3 m in the Wema area (see Fig. 1).

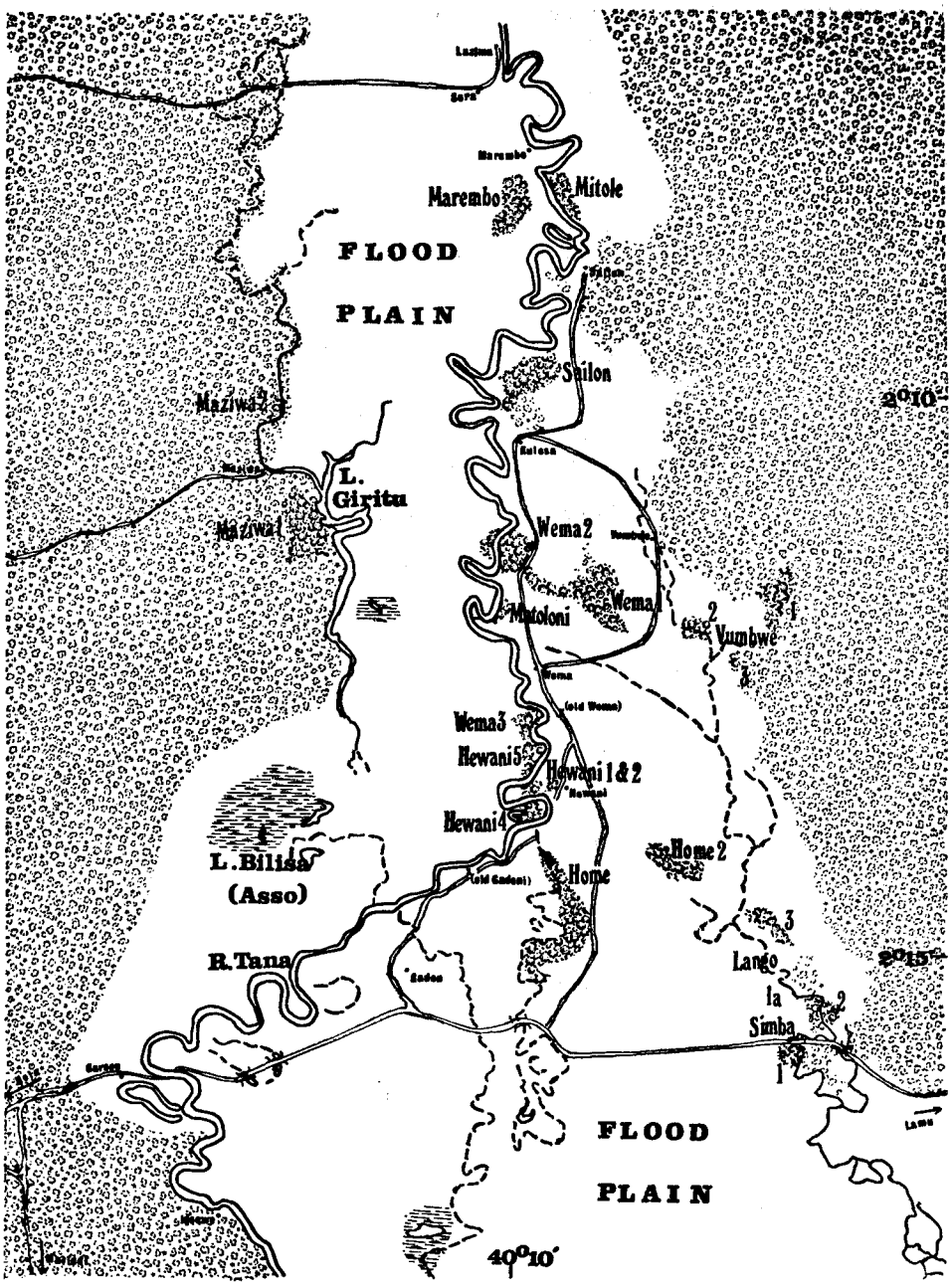

Fig. 2. The southern forests of the 1972 expedition, between Hewani and Mitole. The floodplain is shown in white and is bordered on both sides by bushland (hatched). Old river channels are shown by dashed lines.

The water speed averages 3-4 knots (5500-7400 m/hr), but in the narrowest part, below Wema, reaches 5 knots (9260 m/hr) (Denhardt and Denhardt, 1883). It should be noted that the river has found a new course below Wema since the Denhardts' day, but is still at its narrowest and swifted in this area. Upriver the flow is 2000 cu. sec., but since the lower river receives no tributaries its flow is halved by the time it reaches the sea (Prins, 1952).

In most years the river rises and overflows its banks, the floods remaining high for several weeks. These floods correspond to the rainy season inland, which fills up the upper course of the river, and are not significantly affected by the locay rains. In 1972, the year of our expedition, the river did not flood during the March-May rains but it did flood during the November-December rains. Water was then thigh-deep in Mnazini I, and the river was 8 km wide at Garsen. Twenty-three centimetres of mud, clay and sand were deposited throughout the forest (Katherine Homewood, pers. comm.).

Normal flooding covers the land several kilometres across, often breaking through the banks especially at the stronger bends, and forming broad discharge channels. Some of these follow lines of old river courses; others empty into permanent lakes, such as Lake Bilisa near Garsen and Lake Shakababo near Ngao (see Fig. 1). The floods inundate the gallery forests below Wenje, and kill most of the undergrowth; for this reason the understorey of nearly all the forests consists of saplings only, with little leaf litter and ground cover. The major exceptions to this are the Wenje forest itself and parts of the home forest near Hewani (see Figs. 2 and 3).

The Tana today flows into the sea at Kipini (see Fig. 1); this is not its natural mouth, but the mouth of a small creek, the Ozi. The Tana's own mouth was some 32 km down the coast, but in the 1860's the Sultan of Witu had a canal cut from Belazoni, on the Tana, to join with the Ozi, thus making the Tana itself navigable from Kipini. In 1895 the District Officer at Kipini had the canal widened as a famine relief project; shortly after this an unusually heavy flood carved a very wide channel and the Tana henceforth entered the sea via the Belazoni Canal and the Ozi. The original mouth at Mto Tana ceased to function except during floods when the whole area below Ngao takes on a delta appearance (Williams, 1962; Denhardt and Denhardt, 1884).

Higher up the river, between Garsen and Hola, the Tana has probably been restricted to the present flood plain for some time. There are a number of ox-bow lakes along the course; one such, at Garsen, was probably cut off in the 1961 floods (see Fig. 2). The flood plain is, however, dotted with old channels. Apart from the Ozi, there are four major old courses: one to the west of the present river, and three to the east (see Fig. 2).

The western channel is dry for most of the year except over a 5 km stretch on its southern part. This permanent water is known as Lake Giritu, although the people of Maziwa (the only village along it) are aware that it was at one time the Tana River. There are two forest patches along the "Lake", one of them large (see Fig. 2). On the eastern side of the river, a channel can be made out from Vumbwe as far south as Lango La Simba. A fragmented series of channels go south and east from Lango La Simba to join the Ozi at Kau (see Figs. 1 and 2). West of this channel is one which leaves the Tana just south of Hewani and runs a tortuous course south, beside and occasionally in and out of the expedition's Home Forest. The villagers of Hewani refer to it merely as "Dsanakai" (old river), but it was formerly called Ntumba ya Mudando (Mikael Samson, quoted in Darroch, 1943). South of the Malindi-Lamu road, this channel appears to merge into the third of the eastern channels, which leaves the Tana near Gadeni, and rejoins it somewhat above Ngao (see Figs. 1 and 2).

The question arises: how long has the Tana flowed in its present bed? On the available evidence it was in its present course in the 1870's (Samson, quoted in Darroch, 1943). Prior to that it would appear that the river flowed down the Ntumba ya Mudando channel beside the Home Forest some 150 years ago, and had done so for several hundred years. Earlier still, the Tana flowed past Lango La Simba into the Ozi at Kau. The

Giritu course presumably antedates even this, for there is no mention of it in Pokomo traditions.

Climate

The climate in general is hot and dry. The heat is mitigated during the middle six months of the year by the south-east monsoon which blows regularly almost every day. There are no permanent weather stations in the flood plain area, and the only sources of information are the readings taken by the Denhardts (Denhardt and Denhardt, 1884) and the stations at Malindi to the south, Lamu to the north, and Hola (Galole) inland. The Denharts recorded an air temperature for the area of 18-28°C, rising only 3-5°C in the "hot season", and falling by 10-15°C at night. These figures are somewhat lower than the very consistent recordings of the three weather stations, which range from 23-30°C at the coast and 22-34° at Hola; but given that the inland temperatures are more variable than the coastal, as well as slightly higher, there need be no major discrepancy.

Rainfall is concentrated in one main rainy season, in May and June. There is a minor rainy season at the end of the year, but this is not a constant feature near the coast. Rainfall is highest at the coast and drops off rapidly inland. The total rainfall at Hola is less than half that of the two coastal stations. The study area on the Tana River would, therefore, have rainfall less than that on the coast but more than that at Hola, approximately between 50 and 100 cm; but even the highest figures would not be sufficient to support the evergreen forest found there in the absence of other factors.

One of these factors, on which there are no quantitative data, might be the heavy dewfall. We found that at Bura the dewfall was negligible, but farther downstream, for instance at Baomo, Mnazini and Hewani, it was extremely heavy. Whether this is a correlate of the depth of the water table or of proximity with the sea is not known, but certainly some of the moisture might be expected to be retained in a forest by condensation and dripping from the leaves. As a regularly nightly feature, this could add considerably to the available water. Possibly linked with it is the degree of cloud cover which is less at the coast than inland.

Wind speeds at the coast are remarkably constant. At Malindi they range 4 to 6 knots in the morning, and from 5 to 7 knots in the afternoon. At Lamu they are higher and more variable, ranging up to 17 knots in the evening. These high wind speeds, combined with the lack of cloud cover allowing many hours of sunlight, would seem to make for high evaporation rates, far exceeding the rainfall. Under these circumstances it is hard to see how there could be any coastal forests at all unless they depend on ground water. This is undoubtedly the case with the Tana River forests, which are to be found only in the river flood plain.

Soil

The soils on the Tana River flood plain are in general heavy black clays ("black cotton soils"). When wet they swell up and quickly become impervious to water, so that they are poorly drained and become waterlogged. When dry they develop deep cracks. Even when the soil is apparently very dry, much water is retained in the capillary pores against the draw from the plant roots, so that the plants experience drought even when plenty of soil moisture remains. These clay soils are alkaline, with a *p*H of around 8, and show signs of salt accumulation with high sodium concentrations (2 to 3 per cent). Carbon and nitrogen proportions are low, particularly the latter, which by agricultural standards is greatly deficient. The vegetation is typically grassland or bushland.

In places the soil is noticeably more sandy and lighter in colour. The surface of the ground does not become cracked as it does with the black clays, and the soil is better drained. All of the six villages with which we were familiar in the Hewani area are built on this type of soil probably because of its better drainage. The soil is less saline than the

clays, although the sodium proportion is still high and the *p*H is only a little less. Nitrogen is abundant at the surface of the soil but deficient lower down. Rather surprisingly the carbon content of this soil apparently increases with depth to below 20 cm, but it is not known how far down this extends. The vegetation on this soil is bushed grassland, but it is probable that formerly it was some type of forest or woodland.

The soil in some woodland areas is a mixture of the two above types, with black clays near the surface and lighter coloured sands below 30-40 cm. There is some sodium accumulation; nitrogen and carbon percentages are low.

In forest habitats the soils are relatively more sandy, and are richer in nutrients and organic matter. There is a thin leaf litter and below it is a humus layer only 4-5 cm in thickness. These have low *p*H levels just over 7, low sodium percentages, relatively high potassium and calcium percentages, and high nitrogen and carbon levels. Below about 10 cm the organic content of the soil drops abruptly to less than one eighth of the value in the humus layer. Calcium and potassium levels drop by a half, but the sodium level increases by a factor of three to near toxic level. The soil stays like this to a depth of about 40 cm, and below this the sodium level starts to rise still further, reaching a value of 4 per cent at depth of 70 cm. At this depth the soil becomes darker in colour and has a higher clay content. It weathers like the black clay grassland soils, and mineralogically they are similar. It seems likely that the forest owes its existence, at least in part, to the sandy nature of the soil, by which drainage is improved, leaching promoted, and the accumulation of sodium salts to toxic levels prevented.

In view of the vegetation zonation of the Home Forest, a relative height profile was surveyed across the widest part of the forest, and soil pits were dug at various points along it so as to sample the soil under the different tree associations. It was found that there was an increase in elevation of 5.9 m over a distance of 460 m from the eastern edge of the forest to the highest point in the profile, which was 50 m from the western edge of the forest and 160 m from the old river channel bordering the forest to the west (see Fig. 3). It is possible that the forest is situated where it is because of the slight increase, raising it above the flood level when the Tana floods; but it is also possible that the increase has been brought about by the forest itself by deposition of organic matter.

The soil pits show a soil zonation that parallels that of the vegetation. To the east of the forest in the grasslands, the soil has a high clay content and has the appearance of a black cotton soil; the same is true of the soils in the bushland belt between the forest and grassland. Beyond the fringing bushland is a belt of *Mimusops* woodland which has black soils with high clay content in the top 30-40 cm of the profile, but below that the soil is much lighter in colour and has a high proportion of sand. In the main forest areas the soils vary from light brown to dark brown and have a high sand content. This sequence, although only tested along one line, suggests another explanation for the formation of forest in this area, namely that the increasing sandiness of the soil would be correlated with more luxuriant tree growth. In fact the nearby presence of the old river channel is indicative of both increased sandiness of the soil and improved local drainage (J. B. Gillett, pers. comm.) The profile measured across the forest shows the correlation between these factors (see Fig. 3).

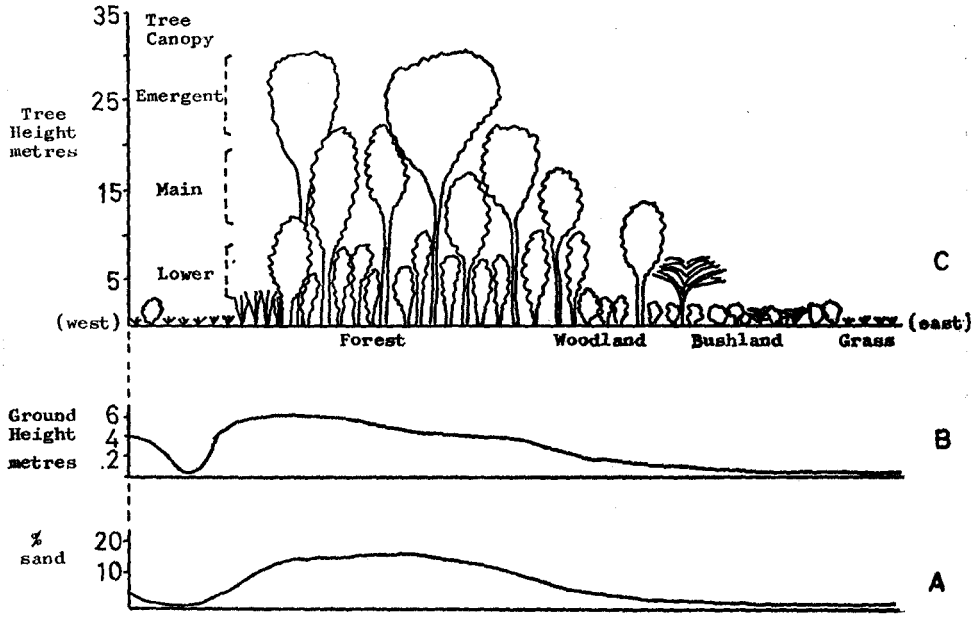

Fig. 3. Structure of the Home Forest: east-west profile showing; A. soil profile expressed in terms of percentage of sandiness of the soil, B. height profile of the surace of the ground, and C. vegetation profile.

TABLE 1

Species lists of plants found along the Tana River

Grassland	*Bothriochloa glabra* (Roxb.) A. Camus
	Echinochloa haploclada (Stapf) Stapf
	Setaria splendida Stapf
	Panicum maximum Jacq.
	Sporobolus confinis (Steud.) Chiov.
	Digitaria adscendens (H.B.K.) Henr.
Bushland and bushed grassland	
Shrubs	*Thespesia danis Oliv.*
	Lamprothamnus zanquebaricus Hiern
	Carissa edulis (Forsk.) Vahl
	Allophylus sp.
	Acacia zanzibarica (S. Moore) Taub.
	Terminalia sp.
	Rhus natalensis Krauss
Trees	*Acacia stuhlmannii* Taub.
	Acacia robusta Burch.=*A. clavigera* E. Mey.
	Tamarindus indica L.
	Terminalia spinosa Engl.
Palms	*Borassus aethiopum* Mart.
	Hyphaene coriacea Gaertn.
Woodland type A	
Trees	*Acacia robusta* subsp. *usambarensis* Burch.
	Mimusops fruticosa A. DC.
	Diospyros mespiliformis A. DC.
	Ficus sycomorus L.
	Garcinia livingstonei T. Anders.

	Sorindeia madagascariensis DC.
	Cola clavata Mast.
Shrubs	*Rinorea ilicifolia* (Oliv.) O. Ktze.

Woodland type B

Trees	*Cynometra* 2 species
	Garcinia livingstonei T. Anders.
	Diospyros abyssinica (Hiern) F. White
	Mimusops fruticosa A. DC.
	Strychnos sp.
	Haplocoelum foliolosum (Hiern) Bullock
	Lannea stuhlmannii (Engl.) Engl.
Shrubs	*Diospyros natalensis* (Harv.) Brenan
	Thespesia danis Oliv.
	Eugenia sp.
	Maytenus sp.
	Bridelia micrantha (Hochst.) Baill.

Lowland evergreen forest—natural forest

Trees	*Sorindeia madagascariensis* DC.
	Celtis wightii Planch.
	Diospyros mespiliformis A. DC.
	Diospyros abyssinica (Hiern) F. White
	Cordia goetzei Guerke
	Pachystela brevipes (Bak.) Engl.
	Gyrocarpus americanus Jacq. subsp. ***americanus***
	Garcinia livingstonei T. Anders.
	Cola clavata Mast.
	Oxystigma msoo Harms
	Sterculia appendiculata K. Sch.
	Ficus sp.
Shrubs	*Polysphaeria parvifolia* Hiern
	Harrisonia abyssinica Oliv.
	Rinorea ilicifolia (Oliv.) O. Ktze.
	Diospyros natalensis (Harv.) Brenan
	Rubiaceae
Lianes	*Pterolobium stellatum* (Forsk.) Brenan
	Paullinia pinnata L.
	Harrisonia abyssinica Oliv.
Palms	*Borassus aethiopum* Mart.
	Hyphaene coriacea Gaertn.
	Phoenix reclinata Jacq.

Lowland evergreen forest—cultivation forest

Mangifera indica L.
Ficus sycomorus L.
Trichilia roka (Forsk.) Chiov.
Bridelia micrantha (Hochst.) Baill.
Diospyros natalensis (Harv.) Brenan
Harrisonia abyssinica Oliv.
Polysphaeria parvifolia Hiern.
Phoenix reclinata Jacq.
Alangium salviifolium (L. f.) Wangerin subsp. ***salviifolium***

Vegetation

Most of the flood plain is covered with grass. There are, however, extensive areas of bushland, rather less woodland, and a few patches of forest. These types will each be described in turn.

Grassland

On parts of the flood plain grassland may be a naturally occurring edaphic vegetation type. Seasonal flooding and poorly drained soils are important factors, and where they

occur it is unlikely that grassland has replaced any other vegetation type. On the other hand it can be seen that ecological disturbance, especially the annual burning carried out by the Orma pastoralists, causes grass to encroach on woodland and bushland, and much of the flood plain may at one time have been covered by bushland.

There were at least three types of grassland recognised on the Tana flood plain. The most widespread type on the heavy black clays is dominated by *Echinochloa haploclada*, which occurs together with *Setaria splendida*, *Bothriochloa glabra* and several other less common species. These are species widely spread in tropical Africa in areas liable to flooding. This grassland type was divided into sharply delineated regions; in some regions the grass was still green at the height of the dry season, and in other regions it was brown and dried up, even though the same species were present in both. Presumably the difference was due to variations in groundwater level or soil distribution.

In places where the surface soils were noticeably more sandy, the grass species were found to be quite different. Two divisions of this type were recognised, dominated respectively by *Digitaria adscendens* and *Sporobolus confinis*. It is likely that flooding is less severe in such areas, as neither of these species grow in very wet places.

The third type of grassland is the tall grass community bordering many patches of forest. Only one species is common here, *Panicum maximum*, and it grows very tall, over 2 m in places. This grass was also still green in the dry season, and when the short grass areas were being burnt near the Home Forest the *Panicum* grassland acted as a buffer preventing the spreading of fire into the forest.

In places, but not further inland than the latitude of Kulesa, the grassland was dotted with palms, especially *Hyphaene coriacea* (doum palm) and *Borassus aethiopum* (borassus palm). In places, both these grew within the forest; and towards the coast they formed forest-like associations by themselves (as around Ngao and Kipini).

Wooded grassland

From about Hola to Wenje is a distinctive habitat, with good growth of grass (even in July) and the trees *Dobera loranthifolia* and *Albizia anthelmintica* spaced through it. It is interspersed with bushland and abruptly distinguished from it. There was a noticeable increase here in plains game, especially Peters' gazelle *Gazella granti petersi* Gunther.

Bushland

Thick evergreen bushland occurs on the flood plain in two kinds of situations, and with different species composition. The most common one has the same species as, and often grades into, bushed grassland (see Table 1), the difference being one of density. The trees and shrubs of bushland form a low and impenetrable canopy, and there is little or no herbaceous vegetation. Those of the bushed grassland are more scattered or are in clumps, and there is an extensive ground cover of grass. There are a number of larger trees of *Acacia robusta* and *Tamarindus indica* in the bushland, and they are protected from fire there, but there is no place where these trees become dense enough for a definite bushland-woodland succession to be established. It is probable that the bushland is a naturally occurring flood plain type and that climatic or edaphic changes would be necessary for it to convert to woodland or forest. Grass fires are encroaching on the bushland, converting it to bushed grassland and eventually to pure grassland.

The other kind of bushland is a forest-derived association, following the destruction of forest by cultivation. The species present are the same as those found in the shrub layer of the forest community (see Table 1). Two variations occur, one in which the dominant element is *Phoenix reclinata*, and the other in which members of the family Rubiaceae dominate, together with *Rinorea* species and *Harrisonia abyssinica*.

Away from the flood plain, bordering it on either side along the lower course of the Tana and almost reaching the river itself higher up (above Mnazini), grows *Acacia*/

Commiphora bushland. The distribution of this type of bushland extends far into the arid country on either side. Where it is intersected by flood plains it supports growths of stunted *Suaeda monoica* and *Salvadora persica*. Towards the river the *S. persica* becomes thick and in parts dense, and there are also fairly dense stands of the euphorb *Spirostachys africana*.

Deciduous woodland

Two distinct associations of woodland are present. In physical structure they are similar, having single open canopies and a sparse shrub layer, but the species compositions are distinctive. The most common association (Type A) is characterised by *Acacia robusta* subsp. *usambarensis*, and *Mimusops fruticosa*. The former is particularly common and forms nearly pure stands in places. In this it resembles the more common Kenya woodland species *A. xanthophloea*, but the canopy in the latter is thicker and there is usually a denser shrub and herb layer. In the other, more localised form of woodland (Type B) there is no *Acacia* and only occasional *Mimusops;* it is characterised by an abundance of *Cynometra* species and *Garcinia livingstonei* (see Table 1).

Lowland evergreen forest

In the flood plain region, there are very few areas where true forest can be said to occur. Where it does, it is fragmented rather than continuous. In the flood plain forests there is a fairly continuous main tree canopy in which *Sorindeia madagascariensis* and *Diospyros* species are the most common trees. There is also a continuous lower canopy consisting largely of *Cola clavata* and *Garcinia livingstonei*. In places there is an emergent canopy, but the trees are widely scattered and completely absent in places. The most notable of the emergents, all of which are extremely large, are *Sterculia appendiculata*, *Oxystigma msoo*, and an unidentified *Ficus* species (see Table 1).

The most representative flood plain forest in terms of number of species is the Home Forest near our camp site at Hewani which has nearly all the species listed in Table 1. There are two variations in species composition. One of these is the forest at Maziwa (on the old course of the river, to the west of the present Tana). This is almost entirely dominated by *Garcinia livingstonei*, both middle and lower canopies, and there is a discontinuous emergent canopy of *Sterculia*, *Ficus*, and *Celtis wightii;* the shrub layer is almost non-existent and what there is of it is composed mostly of *Rinorea ilicifolia*. The other variation is Mnazini III, on the east side of the river. This also is dominated by a single species, in this case *Pachystela brevipes*, which together with *Sorindeia* and *Gyrocarpus americana* make up the single main canopy. The lower canopy and shrub layers are similar to those of the Home Forest.

The presence of an appreciable shrub layer seems to be linked with the degree of flooding experienced by the forest concerned. In a forest subjected to regular annual flooding the shrub layer, except for the taller saplings, is drowned, and visibility in such forests tends to be good, of the order of 20 metres or more. Such forests on the other hand have a thin even carpet of leaf litter. Forests not undergoing annual floods have much more undergrowth, severely restricting visibility as well as movement. The Home Forest is more diverse than most others in that parts of it are raised slightly and so not usually flooded, whereas other portions which do flood are clear of undergrowth.

Elephants, too, have a very evident effect on the structure of the forests. Wema II is in part almost totally opened up, with plenty of evidence of constant visitation by elephants.

Evidence that the flood plain forests were at one time more extensive is provided by areas of forest regrowth. This forest that is regenerating after clearing for agriculture is referred to here as cultivation forest, and it is dominated by mangoes and figs with *Trichilia roka* forming the lower storey. The shrubs are the same as those found in natural forest. It seems very likely that when cultivation of a former forest area is finished,

there is a succession back to semi-natural forest through the bushland and cultivation forest stages. The situation is complicated by the mango; this is an introduced tree, and its prevalence in the cultivation forest is probably the result of its being planted when the area was inhabited. Its absence from any of the natural forests seen probably indicates that these forests were already in existence when the mango was introduced to the Kenya coast.

Floral affinities

Many of the trees in the Tana River forests and woodland are those typical generally of riverine and groundwater vegetation in Kenya and Tanzania. A number of these appear to be almost unique to the region and have doubtful affinities with other parts of Africa, notably *Oxystigma msoo* and *Populus ilicifolia*. The latter occurs in the thin forest-like strip on the very edge of the river in the middle course (Bura to above Garissa), but is not a constituent of forests or woodlands on the flood plain, growing singly or in small groups near the river's edge. It occurs only along permanent rivers in the eastern watershed of Kenya: the Tana, Athi and Ewaso Ngiro rivers; and its closest relative today is *P. euphratica* Oliv., a riverine species of the Euphrates (J. B. Gillett, pers. comm.). *Oxystigma* is a genus with predominantly Central and West African species, but *O. msoo* is known from only three localities in eastern Kenya and Tanzania (Brenan, 1967, p. 134). The two common species in the Tana River woodlands both have a mainly eastern distribution. *Acacia robusta* is widely distributed in East Africa, but *Mimusops fruticosa* is restricted to the east coast (Brenan, 1959; p. 118; Hemsley, 1968, p. 53). Others of the riverine species, on the contrary, have a pan-African or even wider distribution, and these also do not indicate any specific affinities of the flora: examples are *Celtis wightii* (Africa to Australia, Polhill, 1966, p. 9), *Gyrocarpus americanus* (Kubitzky, 1969, p. 182) and *Alangium salvifolium* (East Coast of Africa, and Asia, Verdcourt, 1958, p. 2). A few of the Tana forests species occur also in West Africa, but none of the common West African species are present in the Tana forests, although some occur in other East Coast forests. *Garcinia livingstonei, Diospyros mespiliformis*, and *Pachystela brevipes* are all riverine species in the Uganda and East Zaire forests present also in the Tana River forests, but they are all widely distributed and not necessarily confined to lowland forests (Hemsley, 1968). More common forest species such as *Sorindeia madagascariensis, Cola clavata, Cordia goetzei* and *Sterculia appendiculata* are entirely eastern in distribution.

The total number of tree species present in the Tana forests is very small. Of the three examples of flood plain forests given earlier, the Home Forest is largely dominated by *Sorindeia madagascariensis*, the Maziwa forest by *Garcinia livingstonei*, and Mnazini III by *Pachystela brevipes*. Such single species dominance and the small overall number of tree species indicates that the Tana River forests are extremely impoverished. When the distributions of the individual tree species outlined in the preceding paragraph are considered as well, it would appear that the impoverishment has most affected the West African species, species that are common in other eastern coastal forests. We may conclude that either the West African forms were present at one time but have since died out, or else that they never reached the Tana. This latter possibility implies that the eastern coastal forests were populated by floral dispersal via a southern route, and indeed such a route still exists in fragmented form (Kingdon, 1971). In any case, it can be said that the Tana River forests as they exist today are less like their West African counterparts than most other coastal forests, a conclusion not completely consistent with the faunal evidence (see later sections).

The human population

Three main tribal groups live along the middle and lower Tana: Pokomo, Orma and Somali. Two small tribes, the Boni and Sanye, formerly hunter-gatherers, are said to live in the vicinity but they were not encountered by us. The Pokomo, a Bantu-

speaking tribe, are the riverine people *par excellence.* They live by cultivation of rice, maize, bananas and a few other crops, and possess goats, chickens and dogs. The Orma, a branch of the Galla, live intermingled among the southern Pokomo subtribes. The Orma do not cultivate but own large herds of cattle, white and long-horned. They are less nomadic than formerly. The Somali often move into the riverain zone from the desert area, especially on the north bank of the river. Many are still nomadic; others are settled in the villages of other tribes, such as in the Orma village of Gadeni.

We have attempted to assess the likely conservation prospects of the area by investigating trends in human population levels. The presence of numerous cultivation forests along the river demonstrates that forest areas have been partially destroyed for cultivation in times past, and indicates that this might occur again. At Wenje maize plantations are already encroaching deep into the forest, while both at Maziwa and at Mnazini they have expanded almost up to the forest edge. Although the local irrigation schemes now being undertaken at Hewani and Wema will doubtless result in increased agricultural yield per hectare, in the long run crop increases must inevitably depend on expansion of cultivated area with its consequent removal of natural wildlife habitat.

The census data for the Tana River region were examined in the Kenya National Archives, by courtesy of the Ministry of Natural Resources. Three sets of figures are available: 1948, 1959 and 1962; but, with few exceptions, the figures for 1959 are higher than those for 1962, a situation which might be attributed to social disruption after the 1961-2 floods. Since most of the 1962 figures were double-checked and serious inconsistencies were found only for Gwano location, it is these rather than the 1959 figures which will be accepted here. By taking the 1948 figures as a comparison (there is no means of checking these, so they have to be taken at face value) the parameters given in Table 2 are arrived at.

TABLE 2

Population estimates of the Wapokomo of the Tana flood plain region

Location	Total population		Annual increase	Percentage of children	
	1948 census	1962 census	per cent	1948	1962
Kinakomba	1,754	2,644	3.0	44.2	59.3
Gwano	469	698	2.9	46.5	(51.4)
Ndera	1,613	2,075	1.8	42.8	40.3
Salama	1,656	2,497	3.0	42.3	43.6
4 locations	5,492	7,914	2.7	43.4	49.2
3 lower locations	3,738	5,270	2.6	43.2	44.2

It will be seen that, whatever the degree of accuracy involved, the population has undoubtedly increased. The annual rate of increase on the figures given was 2.7 per cent p.a. over 14 years for four locations covering much of the lower flood plain, an increase which compares closely with the current increase rate of 3 per cent p.a. for Kenya's Coast Province, and is also consistent with the percentage of "children" (under 14s?) in the 1948 sample, forming 43.2 per cent of the total. If the figures are to be trusted, the lower dependency load has increased since 1948, and the rate of natural increase should be accelerating. The implications of this for conservation are grave. This is especially ironic in view of the tolerance of the Pokomo themselves towards wild animals, and the appreciation of them which some of them express.

Forests of the study area

The forests and woodlands of the Lower Tana are enumerated in Table 3. The forest types have already been described, but the distribution of the types is of interest.

All of the patches of cultivation forest are along the edge of the present course of the river. There are some areas away from the river where forest has evidently been cleared in the last 100 years and cultivation practised, for instance between Hewani and Wema, but forest is not regenerating in these areas. The inference is that forest only regenerates near the river; away from the river a forest environment may be self-perpetuating but if it is cleared by man it is unable to regenerate.

TABLE 3

Forests and woodlands of the Lower Tana flood plain

Name of forest/woodland	Area (ha)	Type	Presence of: Mangabey	Colobus
Lango La Simba I	1	*Cynometra* woodland	formerly	x
II	2	" "		
III	2	" "		
Home Forest	50	Lowland evergreen forest with single-dominant and woodland zones	x	xx
Home II	5	*Cynometra* woodland		
Hewani I	1	Cultivation forest	x	x
II	1	" "	x	x
III	1	" " (still cultivated)		
IV	1	" "	x	x
V	2	" "	x	x
Wema I	—	*Cynometra* woodland		
II	—	" "		
III	2	Cultivation forest	x	x
Matoloni	1	" "	x	
Sailon	—	Lowland evergreen forest (v. damaged)		
Mitole	5	Cultivation forest	x	x
Ngumu I	2	*Acacia* woodland	x	x
Berlin	5?	" "	x	
Maziwa I	40	Lowland evergreen forest (*Garcinia*)	xx	
II	1?	" "	x	
Mnazini I	30	Lowland evergreen forest with *Acacia* woodland zones	xx	xx
II	15	Cultivation forest	x	x
III	50?	Lowland evergreen forest (*Pachystela*)	x	x
Baomo	—	*Acacia* woodland	x	x
Kimbu	150?	Lowland evergreen forest (*Sorindeia*)	xx	x
Wenje	30	" " with cultivation forest patches	x	

Notes. The list is based on visits and brief surveys to the forests concerned in each case, with the exception of Maziwa II which is included on the basis of statements by local informants.

Under 'Presence of colobus and mangabey', x indicates that the species still occurs there, xx indicates that it is to be found in comparatively large numbers.

The following forests/woodlands have not been seen, and are not listed: Ngumu II, Munyuni, Bubesa, Kinyado, Nguvini, Kipende, Makere ya Gwano. Judging from map outlines, the total area of these would be of the order of 185 ha. Both colobus and mangabey are reputed to occur in most of them.

Two forest areas that are surviving away from the present course of the river are the Home and Maziwa I Forests. The former is on an old river course that was cut off at least 150 years ago; and the latter is on Lake Girita, an even more ancient part of the river course that still has permanent water in the form of a lake. Both these forests show signs of decline. At Maziwa the main forest canopy is regular but it is composed almost exclusively of one species, *Garcinia livingstonei*. There are a few emergent trees remaining, but no prospective emergents were seen in the lower canopies. Parts of the

Home Forest have reached this stage. It is probable that deficiencies in the environment (most importantly lack of water and correlated rise in alkalinity in the soil) are initially translated into decreasing variety of forest species and finally, under extreme conditions, result in complete destruction of the forest.

There was no evidence seen for the new formation of forest patches, but this lack is probably the result of fire. Much of the flood plain is regularly burnt every year, and this destroys the bushland which would be successional to woodland and forest. Some of the woodland areas along the river are almost certainly a late part of such a succession leading to forest; a good example of this is seen in the Mnazini II Forest which is partly *Acacia* woodland, partly *Acacia* mixed with forest trees, and partly closed forest. It can reasonably be inferred that were it not for fire new patches of forest would be in the process of formation along the present river banks.

It would appear from this evidence that the forests of the flood plains are in a state of flux. Away from the river they are dying off, but along the present channel they are regenerating or would be in the process of being formed were it not for the regular burning. Viewed from the perspective of hundreds of years, the pattern emerges of a river continually changing its course, with forest patches that emerge and die off in comparatively short periods of time as the river alters its course. Such a changing environment would put great pressure on the fauna living in it.

DISTRIBUTION OF FAUNA

A total of 47 species of mammal and 230 species of bird were seen in the course of the field season. Many of the contacts were casual sightings, and no attempt could be made to assess the degree of importance in the flood plain ecology.

TABLE 4

Birds of the Lower Tana River

Sequence and taxonomy follow Forbes-Watson (1971). Subspecific names are omitted except when identification was certain. Assignation to a particular habitat of aerial birds such as swallows and swifts is arbitrary. Species marked with an asterisk are widespread in East and Equatorial African forests. Species marked with a double asterisk are usually restricted to Central African lowland forest. n = netted.

Habitats
1 = *Acacia/Commiphora* scrub
2 = *Dobera/Albizia* parkland
3 = River banks
4 = Riverine forest
5 = Perennial grassland savanna

	1	2	3	4	5
Struthio camelus					+
Pelecanus rufescens			+		
Anhinga rufa			+		
Ardeola ralloides			+		
A. ibis			+		+
Egretta intermedia			+		
E. alba			+		
E. garzetta			+		
Ardea melanocephala			+		
A. goliath			+		
Scopus umbretta			+		+
Ciconia episcopus					
Ephippiorhynchus senegalensis					+
Ibis ibis			+		
Leptoptilus crumeniferus					+
Threskiornis aethiopicus					+
Bostrychia hagedash			+	+	+
Alopochen aegyptiaca			+		
Sarkidiornis melanota			+		
Dendrocygna viduata			+		
Gyps rueppellii	+				
G. fricanus	+			+	+

	1	2	3	4	5	
Neophron monachus	+				+	
Gypohierax angolensis					+	
Circaetus pectoralis		+				
C. cinereus		+				
***C. fasciolatus*				+		
Terathopius ecaudatus	+	+	+		+	
**Accipiter tachiro*				+		
Melierax poliopterus	+	+				
M. gabar	+	+				
Kaupifalco monogrammicus				+	+	
Lophaetus occipitalis		+			+	
**Stephanoaetus coronatus*				+		
Hieraaetus dubius					+	
**Aquila wahlbergi*				+	+	
Haliaaetus vocifer			+		+	
Elanus caeruleus					+	
**Macheiramphus alcinus*				+		
Falco cuvieri					+	
F. chicquera					+	
Sagittarius serpentarius		+			+	
Francolinus sephaena	+	+			+	
F. afer					+	
F. leucoscepus			+			
**Guttera pucherani*				+		
Acryllium vulturinum			+			
Otis kori		+				
Eupodotis ruficrista	+					
E. senegalensis		+				
Actophilornis africana			+			
Vanellus spinosus			+			
V. tectus	+	+				
V. lugubris		+				
Charadrius pecuarius			+			
Burhinus capensis					+	
B. vermiculatus			+			
Pterocles decoratus	+	+				
P. lichtensteinii	+					
Streptopelia decipiens		+	+		+	
S. semitorquata					+	
S. capicola			+		+	
S. senegalensis			+		+	
Oena capensis		+	+			
**Turtur tympanistria*				+		
T. chalcospilos			+			
**Treron australis*				+		
Poicephalus rufiventris		+	+			
Tauraco fischeri			+			
Corythaixoides leucogaster		+				
Pachycoccyx audeberti					+	
Centropus grillii					+	
C. superciliosus					+	
Otus scops		+	+			
Glaucidium perlatum		+	+			
**Ciccaba woodfordii*				+		n
**Caprimulgus pectoralis*				+	+	
C. donaldsoni					+	
C. clarus					+	
Apus aequatorialis						
Cypsiurus parvus						
Telacanthura ussheri						
Colius striatus					+	
C. leucocephalus			+			
C. macrourus		+	+			
**Apaloderma narina*				+		n
Ceryle rudis						
Alcedo cristata						
**Ceyx picta*				+		n

	1	2	3	4	5	
Halcyon senegaloides			+			
H. chelicuti		+			+	
**H. albiventris*				+		
H. leucocephala					+	
Merops albicollis		+				
M. pusillus			+			
M. revoilii	+					
M. s. superciliosus				+		
Coracias caudata lorti	+				+	
**Eurystomus glaucurus*				+		
Upupa epops africana	+	+				
**Phoeniculus purpureus*				+		
**P. granti*				+		
P. minor		+				
P. cyanomelas		+				
Tockus nasutus		+				
T. erythrorhynchus	+	+				
T. deckeni	+	+				
T. flavirostris		+		+		
**T. alboterminatus*				+		
**Bycanistes bucinator*				+		
**Lybius melanopterus*				+	+	
**L. torquatus*				+	+	
L. melanocephalus		+				
Pogoniulus pusillus	+	+				
Trachyphonus darnaudii	+	+				
T. erythrocephalus	+	+				
**Indicator variegatus*				+		n
**I. indicator*				+		
**I. minor*				+		n
**Campethera nubica*		+		+		
**C. abingoni*				+		
**C. cailliautii*				+		
Dendropicos fuscescens		+				
Thripias namaquus		+				
Mirafra rufocinnamomea					+	
M. poecilosterna					+	
Eremopteryx leucopareia					+	
Hirundo smithii						
H. senegalensis						
H. abyssinicus						
Motacilla aguimp			+			
Anthus novaeseelandiae					+	
A. melindae					+	n
Tmetothylacus tenellus		+				
Macronyx croceus		+				
M. aurantiigula		+				
**Campephaga flava*				+		
Pycnonotus barbatus		+		+		
Andropadus importunus					+	
Chlorocichla flaviventris				+	+	n
Phyllastrephus strepitans					+	
P. terrestris					+	
**P. fischeri*				+		n
Eurocephalus rueppellii	+	+				
Prionops plumata		+				
P. retzii					+	
**Nilaus afer*	+	+				
Dryoscopus pringlii				+		
**D. cubla*				+		
Tchagra senegala					+	
Rhodophoneus cruentus	+	+				
Laniarius ferrugineus		+			+	
Malaconotus sulfureopectus		+				
M. blanchoti		+				
Lanius cabanisi		+				
L. dorsalis	+	+				

	1	2	3	4	5	
Cercotrichas leucophrys		+				
**C. quadrivirgata*				+		
***Sheppardia gunningi*				+		n
**Cossypha natalensis*				+		n
**C. heuglini*				+		n
***Neocossyphus rufus*				+		n
Cichladusa guttata			+			
C. arquata					+	
Turdoides squamulatus					+	
T. rubiginosus			+		+	
**Bradypterus baboecala*				+		n
Cisticola chiniana					+	
C. galactotes					+	
C. brachyptera					+	
Prinia subflava					+	
Apalis flavida		+	+			
**A. melanocephala*				+		n
Camaroptera brevicaudata			+	+	+	n
C. simplex			+			
Sylvietta brachyura			+			
**Muscicapa caerulescens*				+		n
Melaenornis pammelaina			+			
Bradornis microrhynchus		+	+			
Batis minor			+			
**Platysteira peltata*				+		n
***Erythrocercus holochlorus*				+		
**Trochocercus cyanomelas*				+		n
**Terpsiphone viridis*				+		n
**Nectarinia olivacea*						n
N. amethystina		+			+	
N. hunteri	+	+				
N. mariquensis		+			+	
N. veroxii					+	
N. nectarinioides	+	+				
N. senegalensis		+			+	
***Anthreptes reichenowi*				+		
A. orientalis		+				
**A. collaris*				+		n
**Zosterops* sp.				+		
Serinus mozambicus					+	
S. atrogularis					+	
Pytelia melba		+				
Estrilda astrild			+		+	
Uraeginthus bengalus					+	
Lagonosticta rhodopareia					+	
Lonchura bicolor					+	
L. cucullata					+	
Ploceus subaureus					+	
P. bojeri					+	
P. castaneiceps					+	
P. cucullatus					+	
**P. bicolor*				+		n
**P. ocularis*				+		
P. rubiginosus		+				
P. velatus		+				
Quelea quelea		+			+	
Euplectes ardens						
E. axillaris					+	
Bubalornis niger		+				
Dinemellia dinemelli		+				
Passer gongonensis		+				
Petronia pyrgita		+				
Vidua macroura					+	
**Lamprotornis corruscus*				+		
L. purpuropterus		+			+	
**Cinnyricinclus leucogaster*				+		
Spreo fischeri		+				

	1	2	3	4	5	
S. superbus		+				
Cosmopsarus regius	+	+				
Creatophora cinerea		+				
Buphagus erythrorhynchus	+	+				
**Oriolus larvatus*				+		
**Dicrurus ludwigii*				+		n
D. adsimilis	+	+				

Birds

The list of birds in Table 4 is based on both observation and mist-netting. The 230 species detected would doubtless be considerably enlarged by studies continued throughout the year. In Table 4 the recorded observations are divided up into five habitat types. Many of the species observed were recorded from only one habitat type because of the differences between these habitats.

In the forest it appeared that lack of undergrowth had a marked effect on the abundance of bird species. No tinker-birds (*Pogoniulus* spp.) were seen or heard by J.F.M.H. or by A. Forbes-Watson, although they were evident in the Sokoke Forest, near Malindi in the same period. Only four undergrowth species were netted in the Home Forest (*Bradypterus*, *Phyllastrephus*, and two *Cossypha* spp.), although protracted study would doubtless reveal more. This forest was however remarkable for abundance of the drongo *Dicrurus ludwigii* and the thrush *Neocossyphus rufus*. The forest at Wenje was visited on one day only and yet was found to have a richer avifauna than forests near base camp. There were many mixed species foraging flocks there, such as were seldom observed in the Home Forest. Stands of tall *Ficus* spp. and considerably more undergrowth could account for this.

In the flood plain grasslands, the palm clusters form a distinctive habitat for birds. A belt of *Hyphaena coriacea* and *Borassus aethiopum* at the south end of the Home Forest (a locality known as Mitapani, "the place of the palm-trees") held nesting vultures *Gyps africanus* and falcons *Falco chicquera*.

A few of the bird records are range extensions. *Bradypterus baboecala* subsp. was netted in the Home Forest on 16 and 17 July. It is the first record for the region, and the habitat is unusual for the species. One was collected and the skin is in the National Museum, Nairobi. A male and female of the sunbird *Anthreptes reichenowi* were observed in the Home Forest on 27 August. This represents a range extension of about 160 km northward from the Sokoke Forest, its nearest previously known habitat. Two specimens of the small insectivorus kingfisher *Ceyx picta* were netted in the Home Forest on 15 and 17 July, and, having the blue ear-covert spot, were assigned to the southern African race *natalensis* rather than the northern tropical *C.p. picta*. White (1965) gives the southern limit of *picta* as the Kenya/Tanzania border and the northern limit of *natalensis* as central Tanzania, but more recently Ripley and Bond (1971) recorded the latter in the Sokoke Forest.

Primates

Five species of monkey and two of prosimian were recorded in the Tana River forests and woodlands. In some forests all seven were recorded, but usually one or two appeared to be absent or were not seen.

Colobus badius rufomitratus Peters Tana River Red Colobus

Red colobus are found mainly near the river from Hewani north to Kipende. Away from the present river course they occur only in the Home Forest, where there is a large healthy population, and at Lango La Simba where in February 1972 one of us encountered a considerable group.

The types of forest inhabited by red colobus may be differentiated into large, containing more than one troop, and small, containing most probably a single troop

only. Two factors appeared crucial in determining the presence or absence of colobus in a given forest. The first of these was variety of food species. In the marginal forests to the east of the river (Home II, Lango La Simba II and III, Vumbwe group) the variety of tree species is much reduced; indeed, some of them are virtually pure stands of *Garcinia livingstonei*, and colobus were never seen in these forests. Colobus are also apparently absent from Wema I which is dominated in part by *Cynometra* which elsewhere is eaten by colobus; the main reason for their absence here, and also from Wema II seems to be the dry scrubby nature of the forest which stands, according to J. B. Gillett, on soda-logged soil.

The second factor, which seems to exclude colobus from forests that might have been suitable for them in terms of food, was canopy structure. During certain periods of the day colobus would be found sitting in open, thinly foliaged emergent crowns. Apart from pure sunning, it may be that such rest periods are essential for the animals' digestive processes (Hollihn, 1971). In any case, forests with a closed, continuous canopy and few open emergents—such as the Maziwa forests, Sailon and Wenje—lacked colobus.

Red colobus are easy to observe, their presence being simple to detect (either they sit in the very tops of the trees and watch the observer, or they jump away with a characteristic crashing sound), and one is liable to gain an initial false impression of their abundance. In point of fact it seems likely that mangabeys, though much harder to detect, are at least as numerous as the colobus. Where we were able to obtain fairly accurate estimates or even actual counts of colobus numbers, it appeared that their population density was greater in the small isolated forests than in the larger forests. We can hypothesize that in the small forests food supply would be the only limiting factor, whereas in larger forests the presence of several troops, with the consequent restriction on the use of space, would represent an additional control. Average densities were, for large forests, 2.8 individuals per hectare, and for small forests, 5.75 per hectare. It should be noted, however, that the large forests are by no means homogeneous, and it may be that the lower density is the direct result of this, since only parts of the forest will be habitable. In contrast to this the more homogeneous small forest patches are more completely utilized by the colobus (C. Marsh, pers. comm.). We have therefore divided up the forests known or suspected to be inhabited by colobus, into two groups according to their size (Table 3). The small forests for which we have extrapolated densities and numbers account between them for only 58 colobus—a small fraction of the total. On the other hand, the Mnazini group of forests, for which we have reliable estimates, and the rest of the northern group, consisting of 430 ha, we estimate carry about 1210 colobus, nearly two-thirds of the total, which is probably about 1860.

Cercocebus galeritus galeritus Peters Tana River Mangabey

In view of the supposed greater rarity of the mangabey, and the fact that it is awarded a red sheet in the *Red Data Book*, the colobus taking a white sheet only, we were surprised to find that its distribution is wider than that of the colobus. Mangabeys occur in a number of forests not inhabited by colobus. Apart from a number of small forests along the lower part of the animals' distribution along the river, the main such forests are Maziwa and Wenje. Both of these are large, closed-canopy forests; the tall open emergents favoured by red colobus are uncommon, and there are few open areas. The internal structure of the two is, however, different: Maziwa has little tangled undergrowth, but plentiful leaf-litter and numerous saplings, so that visibility within the forest is good, about 20 to 30 yards; Wenje is full of tangled undergrowth, implying much secondary regeneration uninhibited by floods. At Maziwa it was found that mangabeys emerge from the forest proper, making their way through the bush to feed on an unidentified seed-pod by the lake. Elsewhere they appear to keep strictly within the forest itself.

It is far harder to obtain an accurate estimate of the numbers of mangabeys than of colobus. Our observations at Mnazini lead us to think that about 90 individuals inhabit

the Mnazini I Forest—about the same number as of colobus. For the Home Forest we suggest a lower density; their distribution there is more localised, indeed we had been entering the forest daily for three weeks before we became aware of their presence. At least two troops live in the northern end of the forest, and it seems likely that at least 50 animals inhabit the whole forest. The other forest for which our own observations suggest a plausible figure is Hewani IV; here there is a single small troop consisting of at least five animals. For Wenje we accept the estimate of 90 animals given us by J-P. Simeon, a thoroughly reliable observer. The vocalisations heard there lead us to accept a density of this order. Similar considerations lead us to accept the figure suggested by K. J. Heribai for Maziwa of 160 animals, although this may perhaps be a little too high.

The density of mangabeys in these forests is between 2 and 4 animals per hectare. Based on these densities, and an estimated 733 ha of forest-woodland where mangabeys are known to occur, a maximum population estimate is arrived at of between 1466 and 2932 animals. Current work by Katherine Homewood (pers. comm.) suggests that the lower figure is more likely.

Cercopithecus mitis Wolf subsp. (*albogularis* group) Sykes monkey

This monkey was noted in troops of 6 to 12 in forests as far upriver as Bura, and away from the river in forests between Lango La Simba and Witu, in Witu Forest, inland from Lamu, and along the forests between Bodhei and Milimani; as well as in the bush areas surrounding the forests. Within the forests they were seen mainly in the trees, but at Bura and whenever they ventured into the bush zone (as at Lango La Simba) they were seen on the ground. The alarm call, a harsh "chak", was heard many times in a forest when the monkeys themselves were not seen.

Cercopithecus aethiops (L.) subsp. (*pygerythrus* group) Vervet monkey

This was the only monkey not observed in the forest itself, nor did vervets appear to venture far onto the grasslands. The typical habitat was woodland or thick bush. They also lived in or near cultivated areas wherever trees, including mangoes, were available for hasty retreat. Although different races have been described north and south of the Tana River, vervets seen at Maziwa (on the right bank) were not noticeably different from those commonly observed in the bush zone at the south end of the Home Forest (on the left bank), and these in turn were little if any different in colour from a juvenile male purchased at Vitengeni (on the western edge of the Sokoke Forest), near Malindi, and which lived as a pet and nuisance around our camp during the expedition's stay on the Tana.

Papio hamadryas (L.) subsp. (*cynocephalus* group) Baboon

Baboons were abundant along the Tana itself, and for as far as one went in either direction. They could be seen in a variety of habitats, but chiefly in the vicinity of forest or heavy bush. Troops varied in size from about 30 to at least 100, the latter size being apparently usual in the desert borderlands inland from Lamu. As everywhere, they are fearless crop-raiders.

The baboons of the Tana region and environs are very different from those seen in 1971 in the Usambara Mountains, near the coast of N.E. Tanzania. Though both have the lanky build and relative manelessness of the "yellow" group of subspecies, the Tana baboons are rather less lanky, and darker, browner than the Usambara baboons which are really yellow. Even in adult males, the naked skin on the lateral parts of the rump is pinkish, not blue-black as in other East African baboons, both yellow and olive. This pink colour seemed to vary with locality, being seen on the up-river baboons (near Garissa), and lower down on the left bank, but not in those of the bush country between Garsen and Malindi.

Galago zanzibaricus Matschie Zanzibar bushbaby

Kingdon (1971) has suggested that this is a full species, distinct from *G. senegalensis*, and that supposed specimens of *G. demidovii* from the eastern coastal forests are the juveniles of same species. This appears plausible to us, in that we were able to observe quite closely a bushbaby in the Mnazini I Forest that had legs not very different in colour from the body, and so differed strongly from the typical *G. senegalensis* seen in the bush country.

Small mammals

Traps were set for a total of 1234 trap-nights in flood plain habitats. The total number of specimens caught was 83, giving 6.6 per cent success. Of the specimens caught, 37 were kept and measured. Seven species are represented, six murids and a shrew.

TABLE 5

Summary of trapping yield

	Home Forest	Grass-land	Munazini II Woodland	Hewani IV lake-side	Hewani Village	Total
Acomys subspinosus wilsoni	30	—	8	—	—	38
Thamnomys dolichurus	8	—	—	—	—	8
Paraxerus ochraceus	3	—	—	—	—	3
Praomys natalensis	—	9	3	6	2	20
Arvicanthis niloticus	—	1	—	—	2	3
Rattus rattus	—	—	—	—	9	9
Crocidura sp.	—	2	—	—	—	2
Totals	41	12	11	6	13	83
No. of trap nights	777	220	87	150	—	1234

TABLE 6

Trapping in the Home Forest

Habitat	Trap nights	*A.s. wilsoni*	*T. dolichurus*	*P. ochraceus*
Closed forest	226	9	3	—
Small tree forest	79	3	2	2
Bush forest	265	13	2	1
Grass clearing	50	2	—	—
Mimusops woodland	64	1	—	—
Fringing bushland	28	2	1	—
More than 1m off the ground	65	(1)	(1)	—
Totals	777	30	8	3

Most of the trapping was done in forest conditions, specifically in the Home Forest (see Tables 5 and 6). *Acomys subspinosus wilsoni* and *Thamnonys dolichurus* were the two common rodents occupying all types of forest and apparently extending into the bordering woodland and bushland. Neither of these are specifically forest rodents, and the absence of the forest rodents is in keeping with the impoverishment of the flora. Both are wide-ranging forms in Africa and presumably they have been able to occupy forest habitats in the absence of more strictly forest-adapted competitors. As a result of this the rodent fauna has no specific zoogeographic affinities with any particular region.

Grassland trapping totalling 220 trap-nights was divided between the eastern edge of the Home Forest (64 trap-nights) and the grass surrounding the camp site (156 trap-nights). There was no apparent difference between the two localities. The common rodent was *Praomys* (*Mastomys*) *natalensis*. A single *Crocidura* sp. was caught in a live trap, and one other specimen was found on the side of the grass track leading to the forest.

Woodland trapping was confined to the woodland zones of the Home Forest (64 trap-nights) and of Mnazini I (87 trap-nights). The two rodent species caught represent the two common species of forest and grassland, *A. s. wilsoni* and *P. natalensis* respectively. In this sense the woodland environment is intermediate between forest and grassland.

Finally, some trapping was done in a patch of cultivation forest bordering a small oxbow lake (Hewani IV). 150 trap-nights were put in, and only *P. natalensis* recorded. It seems likely that formerly in this area there had been forest, which was cleared at least 50 years ago according to local recollection. The small mammal fauna would have been wiped out and the area occupied by the grassland species *P. natalensis*. The common village rodent, *Rattus rattus*, was not found.

In addition to the trapping for small mammals, six wire-mesh cage-type carnivore traps were set out for a total of 248 trap-nights: 168 in the forest, 30 in grassland, and 50 at the edge of the rice irrigation scheme. Altogether 10 animals were caught and released: four *Atilax paludinosus*, two *Ichneumia albicauda*, and four *Genetta tigrina*. In spite of the disparity of trapping times, all of these, except for one genet caught in the forest and two mongooses (one of each species) caught in the rice-field, were taken in grassland.

Crocidura sp. White-toothed shrew

A single shrew of this genus was caught in one of our traps; it did not prove possible to identify it. It is apparently a grassland dweller in the Tana River region. Allen and Lawrence (1936) record three species of *Crocidura* from the lower Tana region.

Paraxerus ochraceus aruscensis (Pagenstecher) Huet's bush squirrel

Three specimens of this bush squirrel were caught, all in the Home Forest and all on the trunks of fallen trees. Additionally one of us observed two of this species on a fallen tree-trunk in a different part of the same forest, and a third in the undergrowth behind (some 1½ metres off the ground). This species has an eastern distribution, and is widespread in eastern and central Kenya, Tanzania, and Equatorial Province of Sudan (Amtmann, 1966).

Paraxerus palliatus tanae (Neumann) Red bush squirrel

This was reported by informants to occur at Mnazini, and was probably the one we saw on one occasion at Wenje. This species also has an eastern distribution ranging from Somalia to South Africa.

Thamnomys (*Grammomys*) *dolichurus* (Smuts) Tree rat

This species was found only in forest conditions on the Tana. In one case it was caught more than 1 metre off the ground, but the other trappings were all on the ground. It is widely distributed in tropical Africa and generally lives in thickets and bushes along forest margins (Misonne, 1968). Living in these situations, the destruction or absence of any rodent forest fauna would enable it to move into the forest and colonise the forest niches left vacant. It seems likely that this has been the case on the Tana River. The species has been recorded from lowland evergreen forest in Uganda (Delaney, 1971). It has been claimed that it is replaced by *T. rutilans* in the forest, but this has not happened in that particular Uganda forest, as they both occurred there together.

Arvicanthis niloticus (Desmarest) Grass mouse

Two positively identified specimens were caught in Hewani Village. One other tentatively assigned to this species was caught in grassland on the edge of the ox-bow

lake at Hewani IV. The skin and measurements of this specimen show similarities with *Pelomys*, but the skull was lost and the specimen cannot be definitely assigned. *A. niloticus* is widely distributed in East Africa in grasslands. It is less common in West Africa, but occurs in Uganda and northeast Zaire (Misonne, 1968).

Rattus rattus (L.) House rat

This is now the dominant commensal rat in East Africa, having largely replaced *Praomys* (*Mastomys*) in this role. It was found only in the village houses on the Tana, and in general it is always found associated with man (Misonne, 1968).

Praomys (*Mastomys*) *natalensis* (A. Smith) Multimammate rat

This species reputedly lives in all sorts of environments in East Africa, but at the Tana River it was not found in forest. It was most common in grassland, but it also occupied woodland (where there is a grass ground covering) and lake edges (where there is also luxuriant grass growth). Interestingly enough, it is the commonest species in the Kafue River flood plain in Zambia (Sheppe and Osborne, 1971). In this area also it was found that this species lived only in grassland areas of the flood plain. The species is widely distributed in Africa south of the Sahara (Misonne, 1968).

Acomys subspinosus wilsoni (Thomas) Spiny mouse

This is by far the commonest species in the Tana River forests and woodlands; it apparently does not live in grassland or bush. In general the spiny mouse is considered an inhabitant of arid environments, and in Uganda is recorded only from dry savanna to semi-desert (Delany and Neal, 1966). Along the Kenya coast it has been recorded from the evergreen bushland south of Mombasa by Koch and in Gedi Forest by G. Rathbun (pers. comm. 1972) so that its habitat preference seems here to be quite different. One of the Tana River specimens was caught more than 1 metre off the ground, so that it may have some arboreal tendencies in the Tana River forests. The species is distributed throughout eastern and southern Africa, and the subspecies *wilsoni* is restricted to eastern Kenya (Setzer, 1968).

Lemniscomys griselda maculosus (Osgood) Striped mouse

This species was collected by Loveridge (Allen and Lawrence, 1936) at Wema and Ngatana, but was not recorded by us. Loveridge comments that it seems to be an uncommon species.

Some species of rodent are notable for their absence in the Tana River area. It is surprising that there was no *Thryonomys* in the area, but the same was found for the Kafue River flood plain (Scheppe and Osborne, 1971), and these authors speculated that it was unable to adapt to changing river levels; this would be equally true of the Tana. The absence of *Pedetes*, *Tachyoryctes* and other burrowers is more easily explained, again by reference to the Kafue situation, as due to the heavy clay nature of most of the soil, and its waterlogging after rain, to say nothing of the catastrophic effect of flooding on an underground animal. It was also expected to find the golden rumped elephant shrew *Rhynchocyon chrysopyus* living in the Tana forests. None were found, however, and it seems likely that the cause of their absence can be attributed to the poverty of leaf litter as a result of flooding.

Carnivores

Large carnivores are rare in the Tana River area because of hunting. Some evidence was seen or heard of the presence of lions *Panthera leo* (L.), leopards *Panthera pardus* (L).

and hyaenas *Crocuta crocuta* Erxleben, but none were actually sighted. Three species of viverried were trapped, and two others were seen, and in addition single individuals were seen of bat-eared fox *Otocyon megalotis* (Desmares), golden jackal *Canis aureus* L., and serval *Leptailurus serval* (Schreber) (see Table 7). Most of these hunt in the flood plain habitats, but only the marsh mongoose *Ichneumia albicauda* (G. Cuvier) and large spotted genet *Genetta tigrina* (Schreber) are found there consistently.

Ungulates

Sixteen species of ungulate were seen in the vicinity of the Tana River. Some, like the hippopotamus *Hippopotamus amphibius* L., are found only in permanent water on the flood plain, e.g. Lake Giritu. Another species, the red duiker *Cephalophus natalensis* (A. Smith), was seen only in the flood plain forests and is probably dependent on them for survival in this area. Other species use the flood plain habitats extensively, but their range also goes into the surrounding bushland, for example the topi *Damaliscus lunatus topi* Blaire, water buck *Kobus ellipsiprymnus* (Ogilby), elephant *Loxodonta africana* (Blumenbach) and buffalo *Syncerus caffer caffer* (Blyth). Finally there are several species that are common in the surrounding bushland but which were seldom seen in flood plain, for example oryx *Oryx gazella beisa* (Ruppell), gerenuk *Litocranius walleri* (Brooke), and zebra *Equus burchelli boehmi.*

TABLE 7

Casual sighting of mammals in the Tana River region

	Habitat	Presence on Flood Plain
Galago senegalensis braccatus Elliot	forest	X
Hystrix sp.	bushland	X
Manis sp.	edge of forest	X
Canis aureus L.	bushland	
Otocyon megalotis (Desmorest)	bushland	
Genetta tigrina (Schreber)	forest	X
Viverra civetta (Schreber)	bushland	
Ichneumia albicauda (G. Cuvier)	bushland	X
Atilax paludinosus (G. Cuvier)	river/grassland	X
Crocuta crocuta Erxleben	bush/grassland	X
Leptailurus serval (Schreber)	bushland	X
Panthera pardus (L.)	woodland	X
Panthera leo (L.)	bushland	
Orycteropus after (Pallas)	bushland	
Loxodonta africana (Blumenbach)	forest/bushland	X
Equus burchelli boehmi	bushland	
Diceros bicornis (L.)	bushland	
Potamochoerus porcus (L.)	forest	X
Phacochoerus aethipicus (Pallas)	bushland	
Hippopotamus amphibius L.	river/lake	X
Giraffa camelopardalis reticulata de Winton	bushland	
Syncerus caffer caffer (Spanman)	all types	X
Tragelaphus imberbis (Blyth)	bushland	
Cephalophus natalensis A. Smith	forest	X
Kobus ellipsiprymnus (Ogilby)	bush/forest	X
Oryx gazella beisa (Ruppell)	bushland	
Damaliscus lunatus topi Blaire	grassland	X
Madoqua kirki (Gunther)	bushland	
Litocranius walleri (Brooke)	bushland	
Gazella granti petersi Gunther	bushland	X

DISCUSSION

The most interesting problems associated with the Lower Tana River flood plain are zoogeographical ones. These will be discussed with reference to the geographical distribution of the flora and fauna and with particular reference to the Tana River

Red Colobus and Mangabey, the two primate subspecies endemic to the region. Some aspects of the ecology of the flood plain will then be discussed to see if they throw any light on the zoogeography.

Zoogeographical considerations

It has been seen that the flora consists mainly of endemic eastern forms and several with an East African to Asian distribution. There are a few species with general African distribution, but none that have strong West or Central African affinities. There are several genera that have many West African species and one East African species, notably *Oxystigma*, whose East African species is restricted to the northern end of the coastal forest zone. Finally, there is one species, *Populus ilicifolia*, with northern affinities, its nearest related species living on the Euphrates.

The faunal evidence is partly consistent with this picture. There is a preponderance of eastern coastal forms, but one or two elements are suggestive of other influences.

The fish of the Tana River are eastern forms and lack characteristic nilotic elements. This would seem to rule out any direct river connection between the Tana and the Nile system, including Lake Rudolf (Whitehead, 1959).

The avifauna has a strong endemic element as far as the East African avifauna is concerned. Such open country birds as the grass warbler *Cisticola restricta* (Traylor, 1967), the weavers *Euplectes diadematus*, *Ploceus bojeri* and *P. castaneiceps*, and the pipit *Anthus melindae* have ranges either centred essentially on the Tana or north and south of it on the maritime strip. The starling *Lamprotornis corruscus* occurs in the area in forest and dense woodland. All of these birds have small and circumscribed ranges. Many populations isolated in riverine and coastal forests in the region have even more restricted distributions, such as the weaver *Ploceus golandi* and the owl *Otus ireniae* (Sokoke Forest), the sunbird *Anthreptes pallidigaster*, the pipit *Anthus sokokensis*, and several populations differentiated at the subspecific level.

These isolates clearly show an affinity of the Tana and other northern coastal forests with the Central African lowland forest. The thrush *Neocossyphus rufus* is an example of a relic population of the Tana (where it is found commonly) and coastal forests, separated from the "parent" population in the Central African (Zaire) forest block by about 1000 km. The akalat (robin) *Sheppardia gunningi sokokensis*, endemic to the Sokoke and Tana forests, is closely allied to two other highly circumscribed races in northern Malawi and the Beira area—a remarkable example of disjunct distribution. Two other birds with disjunct ranges that have been recorded from the lower Tana (although not during the present survey) are the sunbird *Anthreptes neglectus* and the warbler *Apalis chariessa* (Keith, 1968). Populations of some other species are endemic to the Lower Tana forests alone, e.g. the owls *Otus scops nivosus* and *Bubo africanus tanae* (Keith and Twomey, 1968).

In the avifaunal list (see Table 4), species marked with an asterisk inhabit forests of several floristic designations and are more or less widespread wherever suitable cover occurs in East and Equatorial Africa. Species marked with a double asterisk are geographically restricted, and their occurrence on the Tana indicates first a distant affinity with the Central African lowland forest and secondly a close affinity with the nearest forest outlier, the Sokoke. Lying 130 km to the south, and separated by savanna woodland and steppe, the Sokoke has been isolated for much longer than the Tana forests, as evidenced by its greater endemicity (Ripley and Bond, 1971).

The mammal fauna also is dominated by forms with eastern relationships. *Cercopithecus mitis* and *Acomys subspinosus* are species widespread in East and South Africa, but the subspecies groups represented on the Tana are of East African coastal affinities. Some species, notably *Galago zanzibaricus* and *Paraxerus palliatus*, are found only in the forest areas along the east coast, through extending as far south as Mozambique or Natal. A few species, notably *Paraxerus ochraceus*, do not extend so far south and instead

occupy a northeastern range (Kenya, Tanzania, into Sudan). There is only one endemic, *Damaliscus hunteri*, and that is not found on the flood plain itself. In contrast to these, the colobus, mangabey and duiker races of the Tana show direct links with Central Africa. In view of the importance of this relationship for zoogeographic studies, each will be described separately.

Cercocebus galeritus is known from Zaire, and extends to the west across the Congo-Ubangui system to Rio Muni. Eastwards, it has not been recorded from Uganda nor from Tanzania, so that there is a gap of over 1,000 km between the Tana population and its closest relatives. The Tana race, *C. g. galeritus*, is externally not strikingly different from that found on the north bank of the Congo River, *C.g. agilis*, being somewhat paler in colour with longer hairs on the brows. No other mangabeys inhabit any of the eastern coastal forests and even those of Uganda, *C. albigena*, belong to a species not closely related to *C. galeritus*.

Cephalophus natalensis is widespread in East and Central Africa from Natal in the south to Somalia (Juba River) in the northeast, and to the Congo and Ubangui Rivers in the northwest. Within this range there are two well-marked subspecies-groups, differing in size, colouration and other features. The *harveyi* group, with its characteristic dark face-blaze and dark legs, is found from the southern highlands of Tanzania, north and northwest. The exact subspecies found on the Tana remains to be determined, but is certainly of the East and Central Africa groups, not the selfcoloured *natalensis* group of the more southerly forests.

The *Colobus badius* case is perhaps the most interesting of all. The eastern races of this species extend from the Zaire forests down the forests bordering the lakes of the western Rift in Uganda and Tanzania, and have three isolated populations further east: the Uzungwa range (Iringa district) in Tanzania; on Zanzibar; and on the Tana. The apparent interrelationships of these three forms, and their relationship with *C.b. tephrosceles* of the Rift Valley lakes, are well brought out by Kingdon (1971): the Uzungwa race *C.b. gordonorum* closely resembles *tephrosceles* but is blacker above, with a tendency for the lumbar region to be red-tinged and for the shanks to be grey-white; the Zanzibar race, *rufomitratus*, is paler, lacks any red on the body, and is essentially a "washed-out" version of *tephrosceles*. The tendency, in addition, for the northerly (Ugandan) populations of *tephrosceles* to be paler than the southerly (Tanzanian) ones, reinforces the conclusion that the Tana and Zanzibar/Uzungwa types of red colobus are related not to each other but to the geographically nearest *tephrosceles* populations.

Combining the data from plants, birds and mammals, then, we end up with a picture of the geographical relationships of the Tana as follows:

1. a large pan-African element; or at least, taxa so widespread in Africa as to be of no use in assessing affinities.
2. an equally large element specific to the eastern coastal forests. This implies that these forests, as a whole, have been isolated long enough from the central African forests to have developed a characteristic facies; and suggests as well that the coastal forests were at one time more continuous.
3. a small component, in plants only, with extra-African affinities.
4. an endemic component, mostly birds, and not entirely forestliving.
5. a small but intriguing element of Central African affinities; not necessarily confined to the Tana forests, but not extending very far south along the coast.

This has interesting consequences for the study of past climates and vegetation patterns in Kenya. The likelihood of a northern forest dispersal route between Central Africa and the eastern coastal region must be considered, in addition to the agreed southern dispersal route which still exists, though patchily, via the southern highlands of Tanzania, the Zambia-Zaire border area, and northern Anglola. Among the primates for example, *Cercopithecus mitis* is evidently a southern-route form, which has pushed as far north along the coast as the Webi-Shebeli system in Somalia; *Colobus angolensis*, another southern-route species, has reached Kilifi Creek (specimens in the British

Museum from Takaungu) but no further; *Colobus badius* may have followed another route and has apparently been replaced along most of the southern route by *C. angolensis;* and *Cercocebus galeritus* has no intermediate populations at all such as would be expected still to remain if it followed the southern route.

It should be emphasised at this point that the "northern route" is so far a working hypothesis only; essentially it is a model proposed to explain the distributions of two species of primate. The alternative—on the basis of the southern route only—would be to suppose that *Cercocebus galeritus* was formerly distributed throughout the north-eastward band of forests running from Lake Tanganika via Lake Rukwa, the Uzungwas, Ulungurus, Ngurus, Usambaras etc., but has since become extinct for reasons unknown throughout this wide area. Similarly, red colobus of the bicolor *tephrosceles-rufomitratus* type would have inhabited this area but were subsequently replaced by conspecifics of the tricolor *kirkii-gordonorum* type. It must be borne in mind that still too little is known of the ecology of either mangabey or red colobus to rule out such a possibility; it is conceivable, for example, that *Cercocebus galeritus* is adapted to forests subject to periodic flooding, and that rivers (such as the Pangani) along the southern dispersal group did at one time regularly flood. It is also possible that different subspecies of red colobus occupy slightly different niches, so might replace one another as the habitat changed.

Ecology of the flood plain

The Tana River flood plain, with its high water table and frequent flooding, is by far the most productive habitat along the north Kenya coast. The ground-water forests of Witu to the north are similar in structure to the Tana forests, but there is a much greater West African element in the flora, and the fauna is less diverse. The Sokoke Forest to the south is richer both floristically and faunistically, and seems to be the centre of endemicity, especially for bird species, for the Kenya coast. In neither of these forests to north and south of the Tana River does the red colobus and mangabey live, and this is hard to explain in view of the greater affinity of these forests with the West African ones than with the Tana River forests.

The composition of the fauna in the grassland areas of the Tana River flood plain has many similarities with that of the Kafue River (Sheppe and Osborne, 1971). The use by large mammal species of the flood plain habitats is limited to those species that live in the region anyway, but the exclusion of certain groups of animals from the flood plain follows the same pattern and can be attributed to the same reason as for the Kafue flood plain (Sheppe and Osborne 1971). Browsing ungulates are in general excluded not only from the grasslands but also from the forests because of the lack of undergrowth; burrowing species that are characteristic of sandier soils are excluded, as are forest-living elephant shrews that build nests of leaf litter; ants and termites are relatively uncommon, and except for one pangolin *Manis* sp. no ant-eating species were seen nor any evidence for their presence.

The forests and woodlands along the Tana River are dominated by the monkeys, of which five species frequently occur in one forest. These are either completely arboreal or at least capable of becoming so, and as a result they are comparatively unaffected by flooding of the forest. The small carnivores seen are also either partly arboreal (e.g. genets) or partly amphibious (e.g. marsh mongoose). The most common forest-living rodent, *Acomys subspinosus*, is not generally considered a forest rodent, but it was found once some distance off the ground, as was the forest rodent *Thamnomys dolichurus*. *Praomys* (*Mastomys*) *natalensis* is the most common grassland rodent, as it was on the Kafue River flood plain (Sheppe and Osborne, 1971), but it was also found on occasion in woodland areas, where it probably takes refuge during the flooding. Most of the forest fauna, therefore, is at least potentially arboreal, and there are none of the ground-restricted animals, such as *Rhynchocyon*, *Petrodromus*, *Lepus* or *Crycetomys*, found elsewhere along the Kenya coast. One exception to this is the red duiker, but presumably this moves out into the surrounding bush when the forests are flooded.

It would appear that these exceptional conditions in the Tana River forests must be related to the survival there of the Central African species of red colobus and mangabey, but the nature of the relationship is still obscure. No other coastal forest has as rich a higher primate fauna as the Tana River: the Witu and Sokoke forests have three species only (including the baboon); the former Kilifi forest and the Jadini forests to the south have four species, increased by one by the black and white colobus (*Colobus angolensis);* and the former lowland forest of the east Usambaras in Tanzania, incomparably richer in every other respect than the Tana forests, had only four species of higher primate. The contrast is puzzling of the rich primate fauna in the Tana River forests, with two Central African species, to the fauna and flora, which indicate lack of Central African influence and are very impoverished even for the Kenya coastal forests, themselves relatively impoverished. The one feature by which the Tana forests differ from those of the other coastal forests is their transient nature. It was suggested in the description of the environment that the forest patches on now defunct channels of the river are slowly drying and that new patches would be in process of formation were it not for fire. This environmental state of continual change is suggested by Katherine Homewood (pers. comm. 1973) to be that to which the mangabeys particularly are best adapted and is the reason for their survival at the Tana River.

TABLE 8

Full names of plant species when not given elsewhere

Dobera loranthifolia (Warb.) Harms
Albizi anthelmintica Brough.
Suaeda monoica J. F. Gmel.
Salvadora persica L.
Spinostachys africana Sond.
Acacia xanthophloea Benth.
Sterculia appendiculata K. Sch.
Gyrocarpus americanus Jacq.

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SUMMARY

The results are presented here of a two month ecological survey of the Lower Tana River, Kenya. The annual floods of the Tana River support a unique assemblage of flora and fauna on the lower flood plain which differs greatly from the rest of the coastal area, where the climate is generally hot and dry. Both pastoralists and agriculturalists inhabit the flood plain and to a certain extent depend on the floods for their living. Edaphic forests and woodlands are scattered along the lower flood plain; these were investigated in some detail as to their plant, bird, and mammal life, and the zoogeography of the region was considered with reference to the two endemic subspecies of monkey—Tana River Mangabey and Tana River Red Colobus—that live there. The ecology of the forests was found to be greatly impoverished, both floristically and faunistically, and this is taken to be sufficient cause for the strongly local element in both flora and fauna, and for the lack of West African species. Faunal routes between the east coast and West Africa are briefly discussed, and it is concluded that the distribution of the two endemic monkeys is not consistent with the evidence of the southern route through Tanzania.

REFERENCES

ALLEN, G. M. and LAWRENCE, B. (1936) Scientific results of an Expedition to rain forest regions in Eastern Africa (with field notes by Arthur Loveridge). *Bull. Mus. comp. Zool. Harvard*, **79**, no. 3.

AMTMANN, E. (1966) *Prelim. Ident. Man. for African Mammals.* **3**; *Rodentia: Sciuridae.* Smithsonian Institution, Washington.

ANSELL, W. F. H. (1968) *Prelim. Ident. Manual for African Mammals* **8**; *Artiodactyla.* Smithsonian Institution, Washington.

BRENAN, J. P. M. (1959) *Flora of Tropical East Africa: Leguminosae, subfamily Mimosoideae.* 1–173.

BRENAN, J. P. M. (1967) *Flora of Tropical East Africa: Leguminosae, subfamily Caesalpinioideae.* 1–230.

DARROCH, R. G. (1943) Some notes on the early history of the tribes living on the lower Tana, collected by Mikael Samson and others. *J. East Afr. Uganda N. H. Soc.* **17**; 244-254.

DELANEY, M. J. (1971) The biology of small rodents in Mayanja Forest, Uganda. *J. Zool. Lond.*, **165**; 85–129.

DELANEY, M. J. and NEAL, B. R. (1966) A review of the Muridae (Order Rodentia) of Uganda *Bull. Brit. Mus. N.H. Zool.* **13**; 295–355.

DENHARDT, C. and DENHARDT, G. (1884) Bemerkungen zur Originalkarte des unteren Tana-Gebietes. *Z. Ges. Erdkunde, Berlin* **19**; 122-160, 194-217.

DORST, J. and DANDELOT, P. (1970) A Field Guide to the Larger Mammals of Africa. Collins, London.

FORBES-WATSON, A. D. (1971) Skeleton Checklist of East African Birds. National Museum, Nairobi.

HEMSLEY, J. H. (1968) *Flora of Tropical East Africa: Sapotaceae.* 1–78.

HOBLEY, C. W. (1920) The Tana River. *Geogrl. J.* **56**; 297–305.
HOLLIHN, K-U. (1971) Das Verhalten von Guerezas (*Colobus guereza* und *Colobus polycomus*), Nasenaffen (*Nasalis larvatus*) und Kleideraffen (*Pygathrix nemaeus*) bei der Nahrungsaufnahme und ihre Haltung. *Z. f. Säugetierkunde* **36**; 65–95.
KEITH, S. (1968) Notes on the Birds of East Africa, including additions to the avifauna. *Amer. Mus. Novit.* **2321**; 1–15.
KEITH, S. and TWOMEY, A. (1968) New distributional records of some East African Birds. *Ibis* **110**; 537–548.
KINGDON, J. (1971) *East African Mammals* **1**. Academic Press, London.
KUBITZKY, K. (1969) Monographie der Hernandiaceen. *Bot. Jb.* **89**; 182.
MISONNE, X. (1968) *Prelim. Ident. Man. for African Mammals* **19**; *Rodentia*. Smithsonian Institution, Washington.
NISHIDA, T. (1972) A note on the Ecology of the Red Colobus Monkeys (*Colobus badius tephrosceles*) living in the Mahali Mountains. *Primates* **13**; 57–64.
PETERS, W. (1879) Ueber die von Hrn. Dr. G. A. Fischer auf einer im J. 1878 in Ostafrika, von Mombas bis in das Pokomo-Land und das südliche Galla-Land, unternommenen Reise eingesammelten Säugethiere *Monatsber. K. Preuss. Aka. Wiss. Berlin, Phys.-Math. Kl.* 1879: 829–832.
POLHILL, R. M. (1966) *Flora of Tropical East Africa: Ulmaceae.* 1–14.
PRINS, A. H. J. (1952) East Central Africa, III: The coastal tribes of the North-Eastern Bantu (Pokomo, Nyika, Teita). *Ethnogr. Survey Africa* (Int. Afr. Inst.), 1–138.
RAVENSTEIN, E. G. (1890) Mr. J. R. W. Piggott's Journey to the Upper Tana, 1889. *Proc. R. Geogr. Soc.* **12**; 129–136.
RIPLEY, S. D. and BOND, G. M. (1971) Systematic notes on a collection of birds from Kenya. *Smithson. Inst. Contrib. Zool.* **3**; 1–21.
SAMPSON, H. C. (1933) The Tana River Region of Kenya Colony. *J. Roy. Soc. Arts.* **84**; 92-111.
SETZER, H. W. (1968) *Prelim. Ident. Man. for African Mammals* **21**; *Rodentia, Murinae: Genus Acomys*. Smithsonian Institution, Washington.
SHEPPE, W. and OSBORNE, T. (1971) Patterns of use of a flood plain by Zambian mammals. *Ecol. Monogr.* **41**; 179–205.
SIMON, N. (1966) *Red Data Book*, IUCN, Morges.
STEWART, D. R. M. and STEWART, J. (1963) The Distribution of some large Mammals in Kenya. *J. East Afr. N. H. Soc. and Coryndon Mus.* **24**; no. 3, 1–52.
TRAYLOR, M. A. (1967) A new species of *Cisticola*. *Bull. Brit. Orn. Cl.* **87**; 45–48.
VERDCOURT, B. (1958) *Flora of Tropical East Africa: Alangiaceae.* 1–7.
VERHEYEN, W. N. (1962) Contribution à la Craniologie comparée des Primates: les Genre *Colobus* Illiger 1811 et *Cercopithecus* Linne 1758. *Ann. Mus. Roy. Afr. Cent. Tervuren, 8°, Sci. Zool.* **105**; 1–255.
WHITE, C. M. N. (1965) A Revised Checklist of Africa Non-Passerine Birds. Govt. Printer, Lusaka.
WHITEHEAD, P. J. P. (1959) Notes on a collection of fishes from the Tana River, below Garissa, Kenya. *J. East Afr. N.H. Soc.* **27**; 167–171.
WILLIAMS, L. A. J. (1962) Geology of the Hadu-Fundi Isa Area, *Geol. Surv. of Kenya*, Rept. no. 52.

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