ECOTROPICA 2: 195–217, 1996
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HABITAT PREFERENCES OF GRASSHOPPERS (ORTHOPTERA: ACRIDOIDEA, EUMASTACOIDEA) IN THE EAST USAMBARA MOUNTAINS, NE TANZANIA, AND THEIR USE FOR BIOINDICATION

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Abstract. During five months research on the ecology of Acridoidea and Eumastacoidea of the East Usambara Mountains in NE Tanzania 37 species were recorded. One of them occurred only in the lowland forests of Longuza, 30 species were recorded from Amani and 25 species were collected during two visits to the separate mountain ridge Mt. Mlinga, near the village of Magrotto. The species from Amani were arranged in ten ecological groups, of which five are dependent on rainforest and four on open habitats (woodland or savanna). One group consists of hygrophilous species. When considering the occurrence of savanna and woodland species as anthropogenic in origin, the ratio of the number of those species to forest-dependent species was used as an indicator for the level of disturbance of the area. The "savanna effect" for Amani was 42%, but differed from site to site. Forests usually had a low savanna effect, which rose towards the forest edge, road edges and cultivations. At Mount Mlinga the savanna effect was higher than at Amani (63%). This was caused by the high degree of disturbance, but also by the warmer mesoclimate at Mt. Mlinga. On the basis of frequency categories, the savanna species from Amani and Mt. Mlinga were arranged in a sequence, which might indicate their climatic tolerance. Of the six groupings, *Trilophidia conturbata* and *Heteropternis couloniana* (group 1) were common in both areas and thus seem to have the highest tolerance of the cool climatic conditions at Amani. *Oxyaeida poultoni*, *Taramassus cunctator*, *Chrotogonus hemipterus*, *Abisares viridipennis*, and *Protanita longiceps* (group 6) were only recorded from Mt. Mlinga, probably because of the warmer conditions in this area. All other species have a lower abundance at Amani than at Mlinga. *Accepted 28 December 1996.*

Key words: *Grasshoppers, bioindication, rainforest, disturbance, Tanzania, habitat preferences, climatic tolerance, conservation, biodiversity.*

INTRODUCTION

The East Usambara Mountains are known for their outstanding position concerning biodiversity and endemism (Rodgers & Homewood 1982). Until now, the majority of papers have dealt with plants or vertebrates (Moreau 1966, Hamilton & Bensted-Smith 1989, Iversen 1991b). Studies on insects were needed to identify the specific invertebrate communities of the submontane rainforest fauna (Rodgers & Homewood 1982). Compared with other insect groups, grasshoppers are taxonomically well known in Eastern Africa. This is mainly due to the excellent work of the Natural Resources Institute (NRI) in Chatham, England. The NRI is preparing a handbook covering the East African grasshoppers, which will probably generate further taxonomic knowledge and provide a good basis for ecological studies. Grasshoppers usually have special demands in vegetation and microclimate (Sänger 1977, Ingrisch 1980). Only very few monophagous species are known (Chapman 1990) most of which are rainforest species (Rowell 1987). Since grasshoppers are important indicator species for environmental studies in Europe (Kleinert 1992), their use for bioindication in tropical regions needs confirmation. The aim of this research was to provide more ecological data on grasshoppers from the East Usambaras and to test their use for bioindication. In addition, distribution patterns of the grasshoppers may provide some information on the remaining questions concerning the insect fauna of the East Usambaras. To identify the habitat preferences of the East Usambara grasshopper fauna, the following questions were posed:

1. Which habitats are occupied by different species in the East Usambaras and which are their natural habitats? What is the present knowledge of their ecology and biology?

2. Which ecological groups can be distinguished? Can those groups be used for bioindication? Which groups or species are indicators for disturbance?
3. Are there differences in the species composition between Mount Mlinga (Magrotto), which has a lowland facies, and the plateau near Amani? Which factors are important in those differences?

RESEARCH AREA

The East Usambara Mountains are situated in the NE of Tanzania near Tanga town between 4°45' and 5°16' S latitude and 38°30' and 38°48' E longitude (Fig. 1). Mt. Nilo, the highest peak, reaches 1506 m. Mt. Mlinga is the easternmost mountain ridge of the East Usambaras. It is 1069 m high and separated from the rest of the East Usambaras by the forested Zigi Valley. Two more separate mountain blocks, Mhinduro and Mtai, are situated farther north (Iversen 1991a). The two study areas were located at Amani (900 m), with its adjacent hills up to 1100 m and an eastern slope down to 400 m, and at Mt. Mlinga (Magrotto) between 700 and 1069 m a.s.L. (Fig. 2). In the west the Lwengera Valley separates the East Usambaras from the West Usambaras, which is the larger and higher part of the Usambara Mountains (~ 2314 m a.s.L.).

As part of the Eastern Arc Mountains (Usagaran basement system), the East Usambaras are much older than the mountains of the Kilimanjaro/Meru region or the Mbeya/Rungwe region, which were formed by volcanic activity at the end of the Pliocene (1 my ago) (Iversen 1991a). They mainly consist of Precambrian basement rocks (Rodgers & Homewood 1982). In the East Usambaras the main faulting

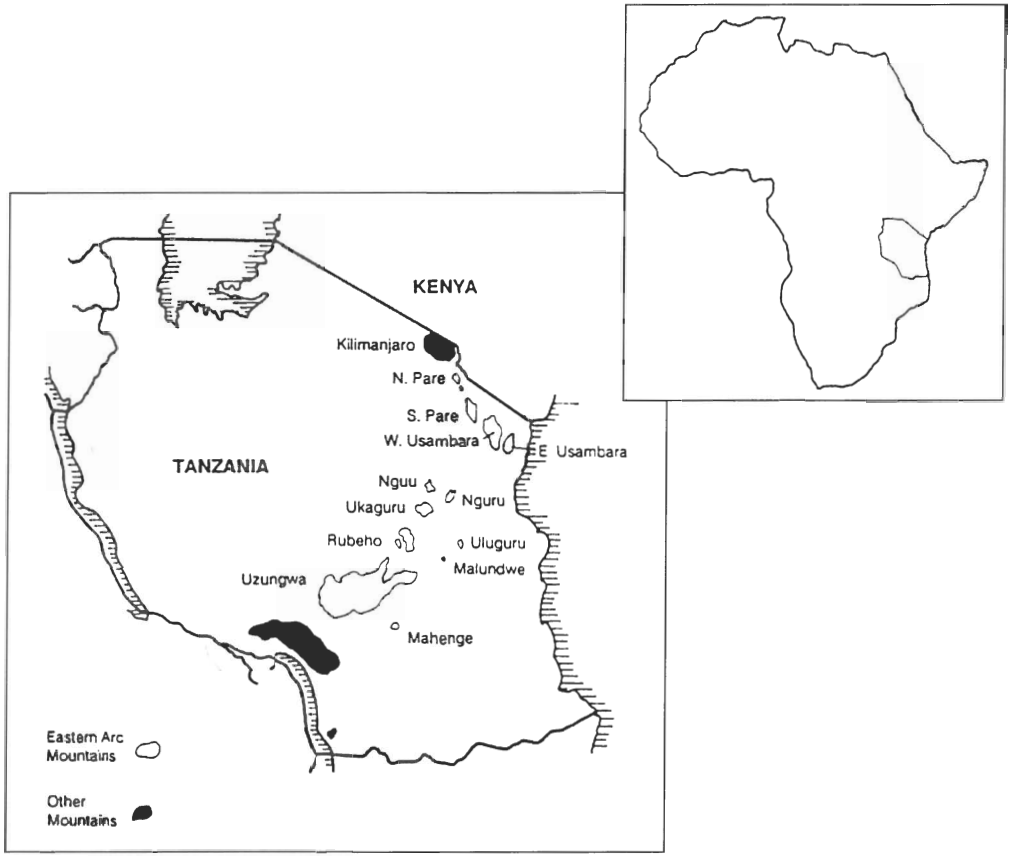

FIG. 1. Location of the East Usambara Mountains and the Eastern Arc Mountains in Tanzania (from Hamilton & Bensted-Smith 1989).

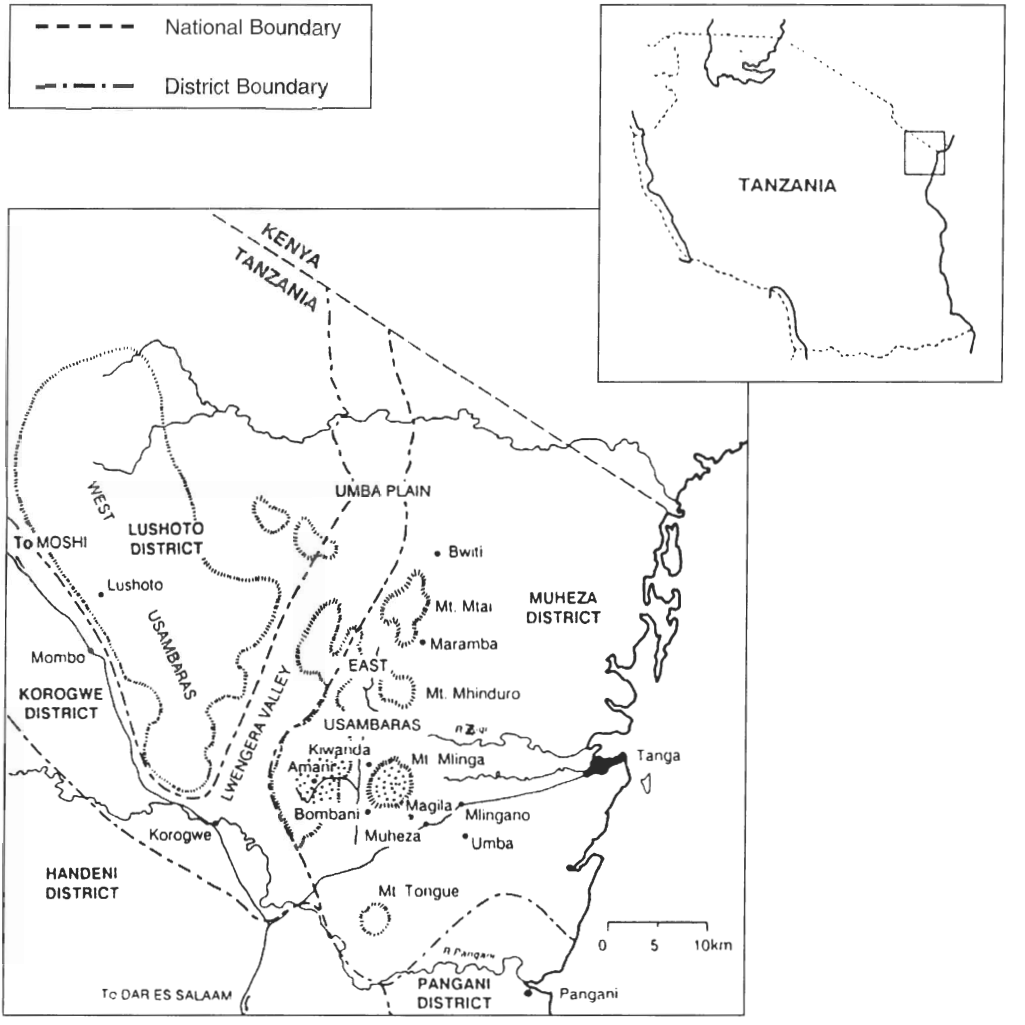

FIG. 2. Location of the Usambara Mountains in the Tanga region (from Hamilton & Bensted-Smith 1989). The two research areas are dotted.

axis is N-S. The date of the latest folding and uplifting has been much disputed. It has been suggested that it was 25 my ago, but other theories date it back only to 2–5 my (Iversen 1991a).

The soils of the East Usambaras are described as red laterite (Phipps 1959) and belong to the humic ferralsols according to the FAO soil classification scheme (Rodgers & Homewood 1982). In the valleys grey-black sandy clay soils occur, which are quite deep and fertile. The soils are undrained and friable. On the escarpments the soils are younger and less leached. They are therefore more fertile than the higher plateau soils (Iversen 1991a), which are very acidic and highly leached (Hamilton 1989).

The climate near the equator is characterized by the occurrence of two rainy seasons, caused by the movement of the Intertropical Convergence Zone. In the East Usambaras a long rainy season lasts from March to May and a short one from November to December (Fig. 3). The long rains provide about 50% of the annual precipitation (Iversen 1991a). The East Usambaras are known to be the wettest area in

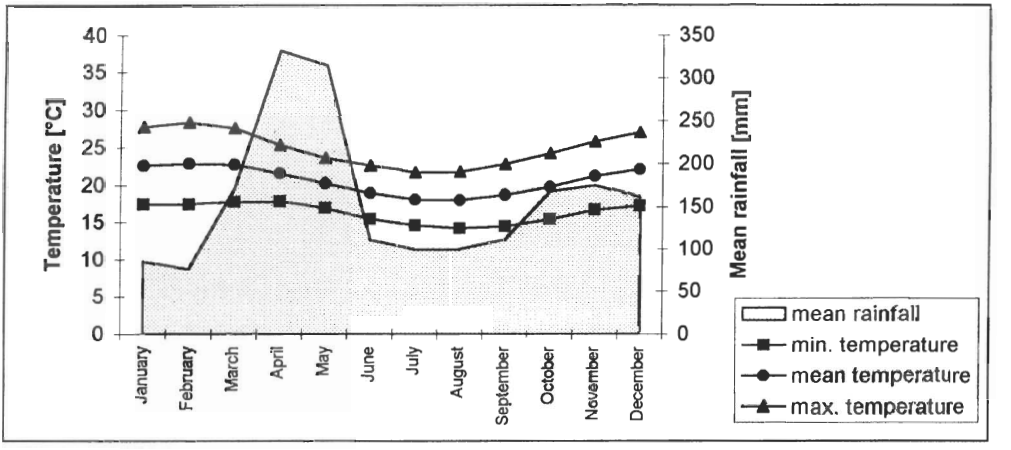

FIG. 3. Mean temperatures and rainfall at Amani 1902–1982 (data from the meteorological Station Amani).

East Africa. They have an average annual precipitation of 2235 mm at Kwamkoro and 1919 mm at Amani (Iversen 1991a); but much variation occurs (Phipps 1959). Amani has an annual mean of 162 rainy days (> 0,25 mm). The climate is humid or perhumid throughout the year with no month having less than 75 mm rainfall (Rodgers & Homewood 1982). Rainfall decreases towards the lowlands and to the North (Iversen 1991a).

The mean humidity is 87% in the morning and 75% at midday (Fig. 4). Fog or mists have been recorded in 130 days annually. Within the forest the humidity is seldom lower than 70%, caused by the dense canopy (Rodgers & Homewood 1982). Light intensity within the forest reaches 0.1% to 0.5% of the outside level. The East Usambaras show exceptionally low temperatures, with the 20°C isotherm passing Amani at 900 m altitude (in the highlands of Kenya at 1400 m). The lapse rate reaches 1.7°C/100 m in the East Usambaras, while the general lapse rate for East Africa has been estimated to be 0.5°C/100 m (Iversen 1991a). The mean annual temperature at Amani is 20.6°C. The mean daily maximum is 24.9°C, the mean daily minimum 16.3°C (Iversen 1991a).

Early descriptions of the vegetation of the East Usambaras give the impression that large parts were forested (Engler 1903). At higher altitudes or on steep slopes heathland, grasslands, bushes and open rocks are more common. In the NW part of the East Usambara plateau, grassy areas with patches of forest were reported. Grassland occurred particularly near the villages, possibly caused by burning (Iversen 1991a).

The forests of the East Usambaras are divided into three types: lowland, submontane and montane forests, but vegetation changes continuously between them (Engler 1903). This results in a complex zonation (Polhill 1968). The montane forest type can normally be found higher than 1500 m. The boundary between the lowland and submontane forest zones has been put at 750 m (Iversen 1991a). Submontane forest is therefore the main forest type of the East Usambara plateau (which is an exception among the Eastern Arc Mountains). Zigi Valley and Mt. Mlinga (Magrotto) have a lowland forest vegetation. Additionally, grasslands and wooded grassland occur, a swamp near Amani and rocky outcrops on the steepest parts of the East Usambaras. Of introduced vegetation, plantation forests (*Maesopsis eminii*, *Tectona grandis*, *Terminalia ivorensis*, and *T. superba*) and cultivated areas (tea plantations, maize, cardamom, cocoyam, sugarcane) are most prominent (Iversen 1991a).

METHODS AND STUDY SITES

The fieldwork was done near Amani between 11 June and 13 November 1994. The study sites are shown in Fig. 5. Thirty-four study sites near Amani were investigated, and are described below. During two visits in 1994, from 27 July to 28 July, and from 13

August to 16 August, the mountain ridge Mlinga was studied at six sites near Magrotto (X1 to X6). The sites were visited during the daytime (only H was also visited at night) and all species of Acridoidea and Eumastacoidea sitting on herbage, shrubs and ground were noted. The recorded species numbers were classified in four categories for every site: Single specimen (1) = one specimen; occasionally (2) = less than ten specimens; dispersed (3) = more than ten specimens in low densities; common (4) = more than ten specimens in high densities.

Notes on the habitat were made. For every month the occurrence of adults was noted. When nymphs were identifiable, their presence was also recorded. The study intensity differed between the sites. The most intensely studied sites were H, N and B. When only a single specimen of a species was recorded, the location of the record was included as a site.

a) Sites near Amani (Fig. 5):

L2: Path through disturbed submontane forest, west of Mbomole hill; forest and forest edge.

P: Zigi Forest Reserve; dense lowland forest.

H: Eastern slope of Mbomole Hill; disturbed submontane forest with clearings and plantations.

M: *Maesopsis*-plantation with forest edge south of EUCODEP-station.

Z: Road through Derema-division; forested part (disturbed submontane forest).

S: Path through dense lowland forest near Zigi river; rich in oilpalms (disturbed).

E: Path from EUCODEP-station to Zigi river; disturbed submontane forest and forest edge.

L: Submontane forest and forest edge at dam north of Amani.

J: Amani East Forest Reserve; dense submontane forest with grassy clearings and forest edge.

W: Eastern forest edge of Mbomole Hill.

C: Western slope of Mbomole Hill; mainly forest edge.

F: Forest edge at Zigi river, south of Site E; banana cultivation.

Q: Path through open-canopied submontane forest between road to Muheza and Derema-division.

V3: Small and open-canopied forest-relict in Derema-division.

VX: Forest edge west of Derema-division.

LL: Cocoyam-banana cultivation in forest north of Mbomole Hill; shrubby forest edge.

I: Edge of road to Muheza; forest edge-like habitat.

B: Swamp north of Amani; partly used for cocoyam and papyrus harvest; hot and humid microclimate with forest edge.

N: Edges of road to Mbomole; forest edge-like habitat with high shrubs, partly more open; dry hot microclimate.

ST: Centre of Amani; open lawns and roads with forest edge.

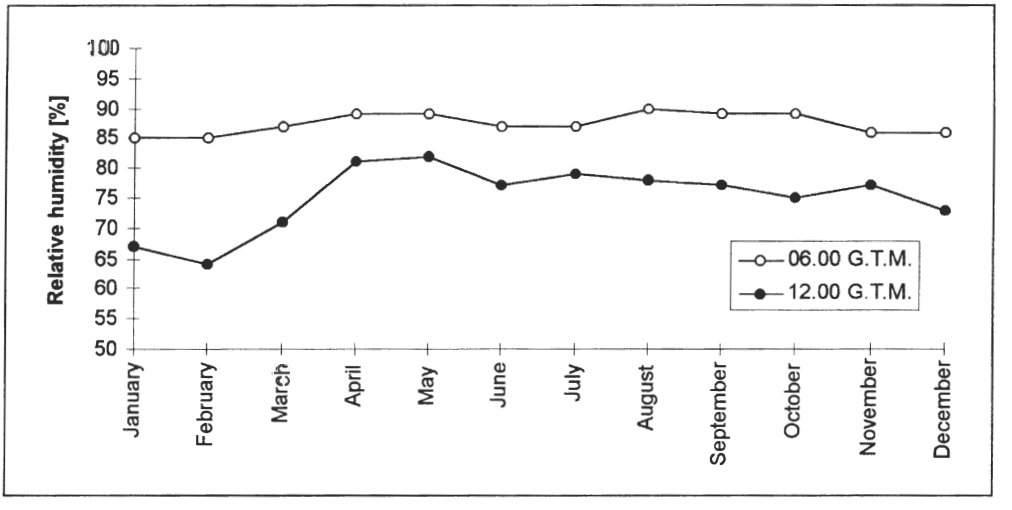

FIG. 4. Mean relative humidity at 6:00 h and 12:00 h at Amani (data from Rodgers & Homewood 1982).

R2: Road to Kwamkoro; forest edge-like habitat; partly dry and hot.
W2: Path through cultivation to Mbomole; partly small forest edges, but mainly open and hot.
V4: Shrubby stream valley in Derema-division; very hot, with shrubs and trees.
G: Top of Mbomole Hill; forest edge with small grassland, rocky outcrops and dense *Lantana camara*-growth.
R: Edge of road at IUCN-resthouse; dry and warm herbage with forest edge.
K: Path through cultivation between Zigi and Amani (F and ST); shaded in the evening, but dry and warm.
D: Road to Monga; forest edge and open road edges, rich in grasses.
Y: Road through cultivations between road to Mbomole and Derema-division; dry and hot, partly shaded.
V: Road through tea plantations in Derema-division; dry and warm.
V2: Continuation of Site V, south of Z to Q; with forest edge.
A: Dry lawn at EUCODEP-office.
VZ: Dry open locations in tea plantations in Derema-division; north of V.
T: Tea plantations west of Mbomole.
U: Road edges west of Mbomole; open and dry.

b) Sites on Mt. Mlinga, near Magrotto:

X1: Open-canopied forest edge at the eastern slope of Mlinga; dense herbage.
X2: Open-canopied forest with cultivation and grass undergrowth; north of X1.
X3: Open grassplain with herbs, between X1 and oilpalm plantation.
X4: Open lawn at Magrotto estate office.
X5: Eastern slope of Mlinga; road to Muheza with dense thickets and herbage.
X6: Oilpalm plantation near lake with grassy undergrowth.

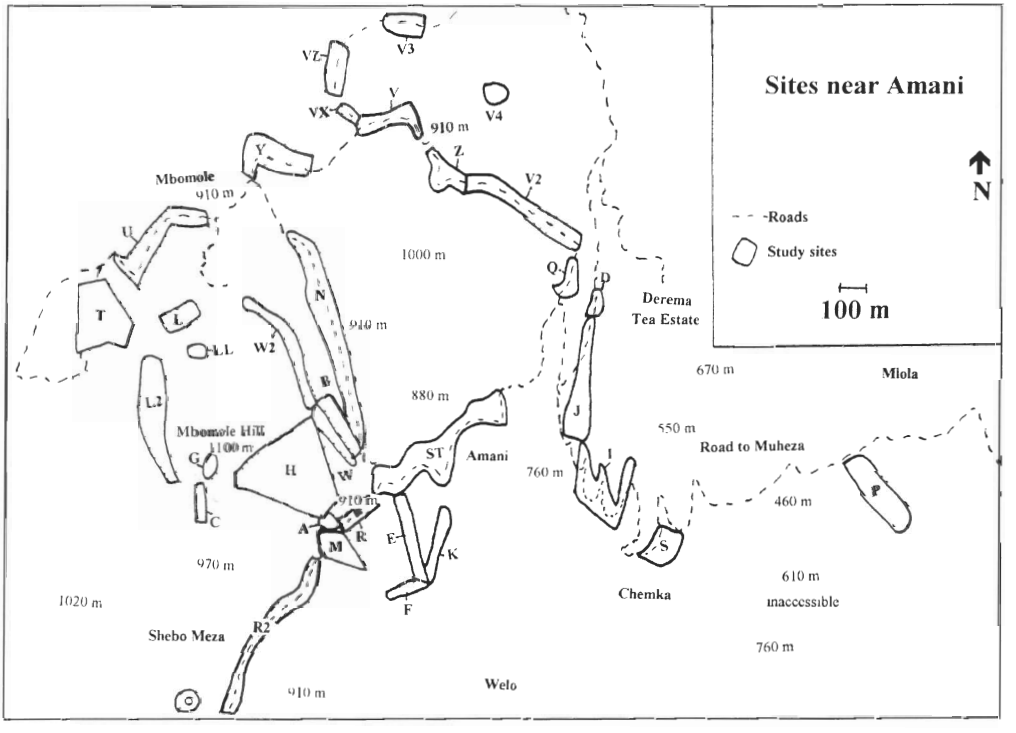

FIG. 5. Location of the study sites near Amani.

All species were identified in the field with the help of a number of publications (i.e., Ramme 1929; Kevan 1959; Descamps 1964, 1973, 1977; Dirsh 1965, 1966, 1970; Hollis 1965, 1971, 1975; Jago 1968, 1981, 1982, 1983, 1984, 1994a, 1994b; Johnsen & Forchhammer 1975; Johnsen 1982, 1983, 1984, 1986, 1987, 1990, 1991; Grunshaw 1991, 1995). Critical cases were checked in the collection of the Natural Resources Institute (NRI), Chatham. Most of the collected specimens have been placed in the collection of the Überseemuseum, Bremen, some at the Natural Resources Institute in Chatham (now transferred to the Natural History Museum, London) and some type material of *Physocrobylus tessa* in the Museum für Naturkunde der Humboldt-Universität, Berlin and in the Zoologisk Museum, Copenhagen.

RESULTS AND DISCUSSION

Species monographs for Amani and Mt. Mlinga

The following species monographs are based on the results from the East Usambaras, on labels of the NRI collection and on literature. Information on localities of records (during this research), ecology, food, life-cycle, and distribution are given.

1. *Stenoschmidtia elegans* DESCAMPS, 1967
Localities: H, J, R2 (3 imagines 06, 08, 09 / 1994; 2 nymphs 09, 11 / 1994).
Ecology: Among ferns and herbs (e.g., *Costus subbiflorus*) higher than 100 cm; but might be a species of the canopy; probably a strict forest species.
Life-cycle: Adults recorded from April to September, but may be present throughout the year.
Distribution: Endemic to the Usambara Mountains (Descamps 1973).

2. *Euschmidtia uvarovi* DESCAMPS, 1964
Localities: J (1 imago 09 / 1994, R. Bischoff coll.).
Ecology: Possibly arboricolous.
Distribution: Only known from the East Usambara Mts. (Descamps 1964).

3. *Plagiotriptus carli* (C. BOLIVAR, 1914)
Localities: H, X3, X6 (1 exuvia 09 / 1994; 3 nymphs 07, 08 / 1994).
Ecology: Found among herbage at the edge of a forest and in the palm plantation; seems to be a species of clearings and forest edges.
Food: Some *Plagiotriptus* species feed exclusively on *Pinus* and *Cupressus* (Uvarov 1977).
Life-cycle: Presumably bivoltine (Phipps 1966).
Distribution: Endemic to the East Usambara Mountains (Descamps 1977).

4. *Mastarammea karaseki* (RAMME, 1925)
Localities: H (1 nymph 09 / 1994, during night excursion).
Ecology: Presumably canopy dweller; at Mt. Rungwe found in high montane forest with giant Lobelias, an area prone to heavy frost at night (Descamps 1977); probably dependent on cool rainforests.
Food: Many *Thericleidae* feed exclusively on ferns (Uvarov 1977).
Life-cycle: Nymphs were collected in September and October, adults in November, December (Ramme 1925, Descamps 1977) and April (Jago coll., NRI collection).
Distribution: Only known from Amani and Mt. Rungwe (Descamps 1977).

5. *Chrotogonus hemipterus* SCHAUM, 1853
Localities: X4 (1 nymph 08 / 1994, 1 adult 07 / 1994), Amani (NRI collection, coll. Jago, 11 / 1964).
Ecology: Thermophilous and confined to dry, open soils; terricolous species; typical for wooded savanna (Johnsen 1990); avoids pure grassland (Robertson & Chapman 1962); probably spread into the Usambaras with deforestation.
Food: Exclusively herbivorous and sometimes damages crops (Voßeler 1905, Johnsen 1982); feeds on *Phaseolus vulgaris*, *Lycopersicum esculentum*, *Gossypium* sp. and *Crotalaria* sp. (Mason 1977).
Life-cycle: Throughout the year, but seems to be more common in the hot season between October and May (Phipps 1966); life-cycle varies depending on microclimatic differences (Phipps 1959); in Tanzania presumably bivoltine (Phipps 1968).
Distribution: Confined to southern and eastern Africa from South Africa to Kenya (Kevan 1959).

6. *Phyteumas olivaceus* (KARSCH, 1896)
Localities: Longuza (1 imago, 08 / 1994).
Ecology: Thicket species (Phipps 1966).
Life-cycle: Presumably univoltine; adults long-lived (Phipps 1966); Hatching is delayed during the rains (Phipps 1968).
Distribution: Endemic to Tanzania (Dirsh 1965).

7. *Loveridgacris impotens* (KARSCH, 1888) (Fig. 7)
Localities: H, N, L2, B (10 imagines 03 / 1993, 06, 07, 08, 09, 10, 11 / 1994), Magrotto (07 / 1994).
Ecology: Occurs very sparsely in the ground litter-layer of the forests; at night and after rain also sitting on herbs; confined to forest and probably highly endangered by deforestation.
Life-cycle: Adults presumably throughout the year.
Distribution: E Usambaras, Nguru Mountains, Shimba Hills and Mrima Hills (Kevan 1950a, 1962, Kevan & Knipper 1961).

8. *Protanita* cf. *longiceps* (I. BOLIVAR, 1904)
Localities: X6 (small population, 07, 08 / 1994).
Ecology: Graminicolous (Johnsen & Forchhammer 1975); presumably typical of coastal grassland; possibly needs high humidity and air temperatures.
Distribution: Tanzanian coast (Kevan 1977).

9. *Zonocerus elegans* (THUNBERG, 1815) (Fig. 17)
Localities: H, R2, G, W2 (16 nymphs 06, 07, 08, 09, 10, 11 / 1994), usually in clumps; N (1 dead imago 06 / 1994); W2 (imagines common 03 / 1993).
Ecology: Occurs in woodland and thickets (Phipps 1968); avoids pure grassland (Robertson & Chapman 1962); in the East Usambaras especially in cultivations near forest edges (Voßeler 1906); naturally not in rainforests, indicator for anthropic disturbance; oviposition in soil (Voßeler 1905, 1907); population size varies considerably from year to year (Johnsen 1982), probably affected by climatic fluctuations.
Food: Mainly herbivorous, but also feeds on Poaceae when other plants are sparse (Johnsen 1990); sometimes damages crops such as cassava, sweet potato, citrus, cotton, sunflower, pigeon pea, tobacco, banana, coffee, cocoa, maize, rice and sorghum; often a severe pest (Voßeler 1904, Johnsen 1982, 1990).
Life-cycle: Univoltine, with adults from October to March (Phipps 1966); at Amani adults usually in March, exceptionally in January (Voßeler 1905, 1907); oviposition in March (Voßeler 1905, 1907); eggs aestivate during the dry season in southern Africa (Robertson & Chapman 1962, Phipps 1968); nymphs hatch from September to December (Voßeler 1907) and pass five instars (Beier 1972).
Distribution: Distributed through southern and eastern Africa (Dirsh 1965).

10. *Atractomorpha acutipennis* (GUÉRIN-MÉNEVILLE, 1844) (Fig. 15)
Localities: B, (nymphs and imagines common 06, 07, 08, 09, 10, 11 / 1994), R2 (1 nymph 10 / 1994), X3 (1 imago 08 / 1994), X4 (common 07, 08 / 1994).
Ecology: Damp areas with high vegetation (Kevan & Knipper 1961, Johnsen 1982); hygrophilous (Descamps & Wintrebert 1969); oviposition in the soil (Descamps & Wintrebert 1966).
Food: Ambivorous (Popov 1989), sometimes attacks sweet potatoes (Phipps 1970), rice (Baccetti & Abukar 1987), egg-plants, tobacco (Johnsen 1982) and other legumes (Descamps & Wintrebert 1969).
Life-cycle: Continuous reproduction with three generations a year in the Sahel (Popov 1989); at least bivoltine in Tanzania (Phipps 1968).
Distribution: Widespread in the whole of Africa south of 14°–16°N, Madagascar, and Asia (Dirsh 1965).

11. *Rhainopomma usambaricum* (RAMME, 1929) (Fig. 16)
Localities: L2, P, H, M, Z, S, E, L, J, W, C, F, Q, V3, VX, LL, I, B, N, ST, W2, G (nymphs and imagines common 06, 07, 08, 09, 10, 11 / 1994); X1, X2, X3 (nymphs and imagines common 07, 08 / 1994).
Ecology: Occurs at forest edges, paths and clearings, among dense and high herbage (Hochkirch 1995); typical of warm and humid lowland forests (Jago 1981); both diurnal and nocturnal (Johnsen & Forchhammer 1975).
Food: Herbs (particularly *Achyrospermum radicans* and *Costus subbiflorus*) and occasionally grasses.
Life-cycle: Nymphs and adults present throughout the year (Phipps 1959, Johnsen & Forchhammer 1975); long-lived (at least nine months); presumably continuously breeding.
Distribution: E Usambaras to Shimba Hills in southeastern Kenya (Jago 1981).

12. *Ixalidium transiens* RAMME, 1929 (Fig. 8)
Localities: H, M, P, S, J, C, N, E, R2, L, B (nymphs and imagines dispersed 06, 07, 08, 09, 10, 11 / 1994).
Ecology: Lives beneath sparse herbage in ground litter of the forest (Hochkirch 1995); at night and after rain on herbs; occurs in primary forests as well as in

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From top left to right down to bottom:

FIG. 7. *Loveridgacris impotens*, sitting on ground litter in Amani West Forest Reserve (H).

FIG. 8. A ♀ of *Ixalidium transiens*, sitting on ground litter in Amani West Forest Reserve (site H).

FIG. 9. *Oxyaeida poultoni*, sitting on a road near Magrotto.

FIG. 10. A ♀ of *Taramassus cunctator*, near the lake on Mlinga Mt. (site X6).

FIG. 11. *Aresceutica subnuda*, at the edge of the road to Mbomole (site N).

FIG. 12. *Catantops melanostictus*, on a lawn near the IUCN office (site A).

FIG. 13. *Heteropternis couloniana*, in the center of a road (site N).

FIG. 14. *Trilophidia conturbata*, at the edge of a road (site N).

Maesopsis eminii plantation; probably needs high humidity and ground litter.
Food: Presumably mainly dead plant debris; in terrarium *Costus subbiflorus* leaves, wet and dry litter and bread.
Life-cycle: Seems to occur throughout the year and breed continuously.
Distribution: Endemic to the E Usambaras.

13. *Ixalidium usambaricum* RAMME, 1929
Localities: X2 (2 imagines 07 / 1994).
Ecology: Probably a strict forest ground species; might occur in warmer conditions than Ixalidium transiens.
Distribution: Only known from Mufoa, Amani and Buloa near Tanga (Ramme 1929); probably endemic to the coastal region near the E Usambaras.

14. *Oraistes luridus* KARSCH, 1896
Localities: X5 (10 imagines 07, 08 / 1994); V2 (1 nymph 09 / 1994, 1 imago 11 / 1994), Zigi near Amani (NRI collection 04 / 1966), between Zigi and Longuza (NRI collection 09 / 1982).
Ecology: Typical of thicket edges and trees (Johnsen 1982); nymphs herbicolous, imagines arboricolous (Uvarov 1977); oviposition presumably in soil; possibly thermophilous; indicator for disturbance.
Food: In the terrarium a nymph fed on *Costus subbiflorus*.
Life-cycle: Presumably univoltine (Phipps 1959); in Tanzania adults from July to April (Phipps 1966); oviposition from January to March (Phipps 1966); eggs develop during the long rains; nymphs present from July to November (Phipps 1959).
Distribution: From Zimbabwe to Kenya (Dirsh 1965).

15. *Afroxyrrhepes procera* (BURMEISTER, 1838)
Localities: K (1 imago 08 / 1994); Zigi (2 imagines, NRI collection).
Ecology: Savanna species; occurs in grassland, woodland and fallowfields (Vesey-Fitzgerald 1964); in long grass (Johnsen 1982); common in cultivations (Descamps & Wintrebert 1969); at Amani possibly not indigenous.
Food: Mainly graminivorous; found on castor, maize, tobacco and Sclerocarya (Johnsen 1982).
Life-cycle: Univoltine (Robertson & Chapman 1962); nymphs hatch from January to March; adults occur nearly every month (Vesey-Fitzgerald 1964), but more abundant from March to June, when oviposition takes place; eggs survive the dry season (July to December) (Robertson & Chapman 1962).
Distribution: Occurs throughout Africa south of the Sahel (Dirsh 1965).

16. *Oxya hyla* SERVILLE, 1831 (Fig. 18)
Localities: B (nymphs and adults common 06, 07, 08, 09, 10, 11 / 1994).
Ecology: Hygrophilous (Phipps 1970); phytophilous (Baccetti & Abukar 1987); mainly in moist grassland (Kevan & Knipper 1961, Popov 1989); Asiatic species of the genus *Oxya* oviposit amongst grasses (Uvarov 1977).
Food: Ambivorous (Johnsen 1982, Phipps 1970); does not seem to attack crops.
Life-cycle: Adults throughout the year; presumably continuous reproduction; number of generations varying from two to four per year (Phipps 1968, Baccetti & Abukar 1987, Popov 1989).
Distribution: Widely distributed in Africa south of the Sahara (Dirsh 1965), Madagascar and the Oriental Region (Hollis 1971).

17. *Parepistaurus pygmaeus* KARNY, 1909 (Fig. 19)
Localities: L2, H, M, E, L, J, W, C, F, Q, V3, VX, LL, I, B, N, ST, R2, W2, V4, G, R, K, Y, V, V2 (nymphs and imagines common 06, 07, 08, 09, 10, 11 / 1994), X1, X2, X3, X4, X6 (nymphs and imagines common 07, 08 / 1994).
Ecology: Forest edge species, occurring in low and dense vegetation (Hochkirch 1995); occupies warm and sunny locations; also in cultivations when some trees are present; mainly recorded from herbs (Hochkirch 1995); active during night and day (Johnsen 1971).
Food: *Ageratum conyzoides*, *Centella asiatica*, herbs and grasses; in terrarium *Costus subbiflorus*.
Life-cycle: Adults presumably throughout the year and breeding continuously; long-lived (at least eight months).
Distribution: Endemic to the E Usambaras and Nguru Mountains (Green, pers. comm.).

18. *Physocrobylus tessa* HOCHKIRCH, 1996
Localities: G, N, C, W, J (11 imagines 06, 07, 08, 09 / 1994; 3 nymphs 11 / 1994).
Ecology: In high herbage at forest edges; most locations with dead herbs and high ground litter; presumably oviposits in soil (Hochkirch 1996).
Food: Seems to be herbivorous.
Life-cycle: One copulation recorded in August; adults possibly throughout the year (Hochkirch 1996).
Distribution: Only known from the E Usambaras (Hochkirch 1996).

19. *Oxyaeida poultoni* RAMME, 1929 (Fig. 9)
Localities: X4, X6 (imagines common 07, 08 / 1994); Zigi-Longuza road (3 imagines 09 / 1982) (Jago 1994a).

Ecology: Open grassland and grassland with bushes (Phipps 1966); usually in dense vegetation (Kevan & Knipper 1961); spreads into sparse vegetation when abundant (Phipps 1959); does not seem to occur in the higher parts of the East Usambara Mts.
Life-cycle: Adults throughout the year; oviposition observed in November and March (Phipps 1959).
Distribution: From central Kenya to northeastern Tanzania (Jago 1994a).

20. *Heteracris coerulipes* (SJÖSTEDT, 1909) (Fig. 20)
Localities: VX, LL, I, N, ST, R2, V4, G, VZ (imagines dispersed 06, 07, 08, 10, 11 / 1994; nymphs 10, 11 / 1994).
Ecology: Thermophilous; often on steep slopes; in high vegetation, such as ferns, bushes and thickets (Phipps 1966); nymphs in herbage at road edges; possibly needs high humidity.
Food: Herbivorous, but also feeds on ferns.
Life-cycle: Adults seem to occur throughout the year (NRI collection); main adult emergence during long dry season (January to March).
Distribution: Distributed through the Tanzanian coastal and submontane forests, e. g., Usambara Mountains, Pugu Hills, Nguru Mountains, Uluguru Mountains, Mlingano, Pangani, Ukami (Grunshaw 1991).

21. *Taramassus cunctator* (KARSCH, 1900) (Fig. 10)
Localities: X6 (imagines dispersed 07, 08 / 1994); Amboni caves near Tanga (1 imago 10 / 1994); Amani (NRI collection).
Ecology: Grassy forest edges and grassland with bushes; in sparse herbage and long grass (Phipps 1966).
Life-cycle: Adults known from May to October (Johnsen 1971).
Distribution: Zanzibar, Tanzanian-Kenyan coast, northern Kenya and Ethiopia (Schmidt, pers. comm.).

22. *Metaxymecus gracilipes* (BRANCSIK, 1895)
Localities: ST, R (2 imagines 06, 09 / 1994); X4, X6 (imagines dispersed 07, 08 / 1994).
Ecology: Graminicolous savanna species (Johnsen 1971); presumably not naturally occurring at Amani; on lawns near houses (short grass).
Food: Possibly graminivorous.
Life-cycle: Univoltine; adults throughout the year (Vesey-Fitzgerald 1964); nymphs from December to March; eggs from July to December (Robertson & Chapman 1962).
Distribution: Widespread through Africa south of the Sahara (Grunshaw 1995).

23. *Aresceutica subnuda* KARSCH, 1896 (Fig. 11)
Localities: H, M, Z, L, J, W, F, Q, V3, VX, LL, I, B, N, ST, R2, W2 , V4, K, D (imagines 06, 07, 08, 09, 10, 11 / 1994; nymphs 08, 09, 10, 11 / 1994).
Ecology: Species of forest edges and clearings; in herbage and on forest floor (Jago 1970); often near paths and roads; diurnal and nocturnal.
Food: Herbivorous; *Solanum robustum*.
Life-cycle: Adults presumably throughout the year; high abundance of nymphs in November.
Distribution: Restricted to north-eastern Tanzania (Buloa near Tanga, East Usambaras) and southeastern Kenya (Shimba Hills) (Dirsh 1965).

24. *Abisares viridipennis* (BURMEISTER, 1838)
Localities: X3, X6 (2 nymphs 07, 08 / 1994); Amboni caves near Tanga (1 nymph 10 / 1994).
Ecology: Woodland species (Johnsen 1982); nymphs among grass and herbvegetation; adults on bushes at thicket edges and in forest clearings (Phipps 1970); arboricolous (Uvarov 1977); oviposition most likely in the soil; abundances usually low (Vesey-Fitzgerald 1964).
Food: Herbivorous (Phipps 1970); found on some crops like cotton, castor, *Erythrina* and *Calotropis* (Johnsen 1982).
Life-cycle: Univoltine (Phipps 1970); adults throughout the year; in Sierra Leone adult diapause (Phipps 1968).
Distribution: Widespread in Africa south of Sahara (Vesey-Fitzgerald 1964).

25. *Catantops melanostictus* SCHAUM, 1853 (Fig. 12)
Localities: V3, R2, V4, R, K, D, V, A, VZ (imagines dispersed 06, 07, 08, 09, 10, 11 / 1994); X3, X4, X6 (imagines common 07, 08 / 1994).
Ecology: Woodland species (Johnsen 1991); prefers coastal lowland conditions with high temperatures and humidity (Jago 1984); occupies dry locations with high grasses (Kevan 1950b, Phipps 1966); in the East Usambaras mainly treeless places near tea plantations and road edges.
Food: Mainly herbivorous (Johnsen 1991); *Geranium* (Phipps 1959).
Life-cycle: Possibly bivoltine (Phipps 1966), adults throughout the year (Johnsen 1991).
Distribution: From South Africa and Namibia to Tanzania and the Kenyan coast (Jago 1984).

26. *Phaeocatantops femoratus* (RAMME, 1929)
Localities: VX, B, R2, V4, V, T (eight imagines 08, 09, 10, 11 / 1994); X2, X3, X4, X6 (imagines common 07, 08 / 1994).

Ecology: Species of coastal woodland; in the East Usambaras in open cultivations, road edges, tea plantations and disturbed forest with cardamom cultivation; indicator for disturbance of forest; in dense herbage, but avoids short grass (Phipps 1959).
Life-cycle: Throughout the year, with lower abundance from September to November; nymphs numerous from March to November (Phipps 1959).
Distribution: Northeastern Tanzania (Tanga, Mlingano, foot of S. Pare Mts., Lushoto) and southeastern Kenya (Shimba Hills, Diani village) (Jago 1982).

27. *Eupropacris pompalis* (KARSCH, 1896) (Fig. 21)
Localities: H, E, W, Q, V3, VX, LL, I, N, R2, V4, D (nymphs common 09, 10, 11 / 1994; 1 K imago 07 / 1994; further imagines 11 / 1994); Zigi (NRI collection, Jago coll., 12 / 1965).
Ecology: High herbage of forest clearings and edges; on *Solanum* (mainly *Solanum robustum*).
Food: Seems to be specialized on *Solanum*.
Life-cycle: Univoltine; adults from November to March; an adult specimen from July probably survived the long rains, but seems to be an exception.
Distribution: Known from Buloa near Tanga, Nguelo; Amani and Zigi (Ramme 1929).

28. *Eupropacris ornata* (KARNY, 1907)
Localities: Z, W, V3, VX, LL, B, N, ST, R2, V4, G, T (nymphs common 06, 07, 08, 09, 10, 11 / 1994, imagines common 10, 11 / 1994); B (imagines common 03 / 1993).
Ecology: Forest edge species; mainly at places with high insolation and high and dense vegetation; highest abundance in a stream valley (B) and a tea plantation (T); predated by a lizard; a nymph attacked by a *Salticidae* spider.
Food: Ambivorous; papyrus and other grasses; tea leaves.
Life-cycle: Univoltine; adults present from October to April (Phipps 1966).
Distribution: Lake Malawi, Zanzibar, Dar-es-Salaam, East Usambaras, Tanga (Ramme 1929).

29. *Acanthacris ruficornis lineata* STOLL, 1813
Localities: B, N, W2, V4, R, VZ, U (imagines occasionally 06, 07, 08, 09, 10, 11 / 1994; nymphs occasionally 10 / 1994); X6 (two imagines 08 / 1994).
Ecology: Mesophilous and phyto-arboricolous (Popov 1989); woodland species (Johnsen 1983, 1991); in the East Usambaras in small groups in cultivations and tea plantations; highest abundance in tea plantation (T); might have immigrated due to human activities.
Food: Ambivorous (Uvarov 1977); found on several crops, such as cassava, castor, pigeon pea, soya, cotton, egg-plant and tobacco (Johnsen 1983, 1991); *Solanum robustum*, tea leaves.
Life-cycle: Presumably univoltine (Phipps 1966); adults throughout the whole year (Dirsh 1970); oviposition from January to March (Robertson & Chapman 1962); seven nymphal instars (Beier 1972).
Distribution: Widespread in Africa south of Sahara, where it occurs with five subspecies (Vesey-Fitzgerald 1964).

30. *Acrida sulphuripennis* (GERSTÄCKER, 1869)
Localities: ST, R (3 imagines 08 / 1994); X4 (2 imagines 07, 08 / 1994); Amani (Jago coll., 11 / 1964, NRI collection).
Ecology: Savanna species; in open grassland; avoids woodland (Robertson & Chapman 1962); in the East Usambaras on open lawns; probably immigrated with deforestation.
Food: Graminivorous (Popov 1989); feeds on dry and coarse grasses (Johnsen 1991); sometimes attacks maize (Harris 1937).
Life-cycle: Univoltine; adults mainly from March to September (Robertson & Chapman 1962); but recorded in all months (Phipps 1966, Johnsen 1991).
Distribution: Distributed throughout Africa south of the Sahara (Dirsh 1965).

From top left to right down to bottom:

FIG. 15. *Atractomorpha acutipennis*, ♀ from Site B (swamp north of Amani).

FIG. 16. *Rhainopomma usambaricum*, feeding on *Costus subbiflorus* (site H).

FIG. 17. *Zonocerus elegans*. A photograph from March 1993 (site W2).

FIG. 18. *Oxya hyla*, at Site B (swamp north of Amani).

FIG. 19. *Parepistaurus pygmaeus*, at the edge of a forest (site W).

FIG. 20. A marked *Heteracris coerulipes* (site N).

FIG. 21. A nymph of *Eupropacris pompalis*, sitting on *Solanum robustum* (site LL).

FIG. 22. *Afrophlaeoba usambarica*, sitting at the edge of a road (site N).

31. *Parodontomelus arachniformis* JAGO, 1983
Localities: J (imagines dispersed 07, 08, 09 / 1994); X2, X6 (07, 08 / 1994).
Ecology: Forest edge species of humid lowland and submontane forest; sunny patches inside forest and at forest edges; on grasses and litter-layer.
Life-cycle: Adults throughout the year; highest emergence from January to March.
Distribution: Zanzibar, in the Shimba Hills, Mrima Hills, Jilore Forest and Gogoni Forest in Kenya and in the East Usambaras (Jago 1983).

32. *Afrophlaeoba usambarica* (RAMME, 1929) (Fig. 22)
Localities: J, F, C, Q, VX, I, B, N, ST, R2, W2, V4, G, R, K, D (nymphs and imagines common 06, 07, 08, 09, 10, 11 / 1994); X3, X6 (nymphs and imagines dispersed 07, 08 / 1994).
Ecology: Species of grassy forest edges and large clearings; predated by an Araneidae spider.
Food: Probably graminivorous.
Life-cycle: Adults present throughout the year (Jago 1983).
Distribution: Endemic to the East Usambaras and adjacent regions (Jago 1983).

33. *Gymnobothroides pullus* KARNY, 1915
Localities: I, N, ST, R, K, V (imagines common 06, 07, 08, 09, 10, 11 / 1994); X3, X4, X6 (imagines common 07, 08 / 1994).
Ecology: Species of open forest edges with grassy vegetation; higher abundance at hot road edges and at Mt. Mlinga; known from lowland and higher altitudes (Jago 1968).
Food: Probably graminivorous.
Life-cycle: Adults presumably throughout the year.
Distribution: Distributed from South Africa to Tanzania (Jago 1968).

34. *Heteropternis couloniana* (SAUSSURE, 1884) (Fig. 13)
Localities: N, ST, R2, W2, V4, G, R, K, D, Y, V, A, T, U (imagines common 06, 07, 08, 09, 10, 11 / 1994; nymphs 10, 11 / 1994); X2, X6 (imagines common 07, 08 / 1994); V (imagines common 03 / 1993).
Ecology: Geophilous and thermophilous savanna and woodland species; also mountain forests (Rehn 1914); adults on dry open ground, such as roads, paths and cultivation; nymphs in short grass (Phipps 1966).
Food: Ambivorous (Phipps 1970, Johnsen 1971).
Life-cycle: Adults present throughout the year (Dirsh 1970).
Distribution: Widespread in the whole Ethiopian Region (Dirsh 1970).

35. *Humbe tenuicornis* (SCHAUM, 1853)
Localities: W2, R (two imagines 06, 08 / 1994); X6 (06 imagines 07, 08 / 1994).
Ecology: Semi-desert and savanna species (Kevan & Knipper 1961); mesophilous and geo- to phytophilous (Popov 1989); occupies sandy habitats (Uvarov 1953); oviposition in bare soil (Johnsen 1986); inhabits grass with moist bare soil patches or around bushes (Phipps 1966); in the East Usambaras on open ground in oilpalm plantations, on paths and at edge of roads; may have immigrated due to human activities; indicator for deforestation.
Food: Exclusively graminivorous (Johnsen 1986).
Life-cycle: Highly variable; two to four generations per year (Lecoq 1978); bivoltine near the East Usambaras (Phipps 1966); embryonic dormancy (Baccetti & Abukar 1987), which is broken by water contact (Uvarov 1977); adults sometimes aestivate (Phipps 1968).
Distribution: Distributed through the whole of Africa, southern Spain and Arabian Peninsula (Dirsh 1965).

36. *Morphacris fasciata* (THUNBERG, 1815)
Localities: ST, W2, V4, R, Y, A, VZ, T (imagines occasionally 06, 07, 08, 09, 10, 11 /1994); V, (imagines dispersed 06, 07, 08, 09, 10, 11 /1994); X3, X4, X5, X6 (imagines common 07, 08 / 1994).
Ecology: Savanna and woodland species; more common in woodland (Robertson & Chapman 1962); strictly geophilous (Popov 1989); always associated with bare soil, nymphs also in short grass (Phipps 1966); in the East Usambaras in road edges, tea plantations and cultivations.
Food: Mainly graminivorous (Phipps 1970); occasionally damages young sorghum and maize plants (Baccetti & Abukar 1987).
Life-cycle: Continuous reproduction (Phipps 1970); adults throughout the year (Lecoq 1978); number of generations varies from one to four per year (Lecoq 1978); in Tanzania possibly bivoltine (Robertson & Chapman 1962); near the East Usambaras peak of oviposition in the long dry season (January to March) (Phipps 1966).
Distribution: Distributed through almost the whole of Africa and southwest Asia (Dirsh 1965).

37. *Trilophidia conturbata* (WALKER, 1870) (Fig. 14)
Localities: N, ST, R2, W2, V4, R, K, D, Y, V, A, T, U (imagines common 06, 07, 08, 09, 10, 11 / 1994; nymphs common 09, 10, 11 / 1994); X1, X3, X4, X5, X6 (imagines common 07, 08 / 1994); V (imagines common 03 / 1993).

Ecology: Geophilous species (Johnsen 1991); at dry, warm patches with sparse vegetation; usually on bare soils; nymphs also in short grass (Phipps 1966); in the East Usambaras in road edges, cultivations and tea plantations; less thermophilous than *Morphacris fasciata*.
Food: Mainly graminivorous, but also on forbs (Johnsen 1986); recorded from leaves of young legumes (Harris 1937) and roses (Phipps 1959).
Life-cycle: Continuous reproduction (Phipps 1959, 1970, Lecoq 1978); adults throughout the year with two generations (Baccetti & Abukar 1987); near the East Usambaras peak of adult emergence during the short rains (October to December) (Phipps 1966).
Distribution: Throughout the whole of Africa south of the Sahara and Arabian Peninsula (Hollis 1965).

Ecological groups at Amani and the "savanna effect"
Grasshoppers are generally divided into ground dwellers (geophilous), grass and herbage dwellers (phytophilous), and tree and shrub dwellers (arboricolous, Uvarov 1977). In this study, only canopy dwellers (eumastacoids) are regarded as arboricolous. Species spending their nymphal stages near the ground and ascending when they become adult should be regarded as phyto-arboricoles. The problem of differing nymphal and adult habitats is quite often disregarded. This is mainly due to the adults being more easily identifiable. Occurrence in different vegetation structures and microclimates results in differing species composition at different sites. In Table 1 the complex of species recorded from Amani is arranged in ecological groups according to their distribution in the study area.

Ten ecological groups can be distinguished, of which five are dependent on rainforest and four on open habitats (woodland or savanna). The status of woodland and savanna species is difficult to judge, but it is likely that some of them also occurred naturally in montane grassland (e. g., *Catantops melanostictus*). Most of the savanna species are favored by human activities, occurring in the study area exclusively at road edges and on cultivated patches. This suggests a former immigration of some savanna species into the East Usambaras as a result of deforestation (*Humbe tenuicornis*, *Acrida sulphuripennis*). Those species can be regarded as forest entrants (Uvarov 1977). An adequate explanation for the widespread character of several savanna grasshopper species in the East Usambaras is Whites' (1978) hypothesis that some savanna species were restricted to specialized sites, from where they spread after forest destruction. The hygrophilous species may have been native to the area near Amani, since an open swamp seems to have existed in the East Usambara Mountains at the beginning of the century (Engler 1908).

According to Iversen (1991b), the main part of the East Usambaras was forested that time. This is particularly true for the southern part of the area, where all of the study sites were located. The savanna species can be regarded as indicators for the disturbance of the area. Most of them would not be able to establish themselves in natural rainforest. The percentage of savanna species occurring in the area might be called the "savanna effect" and may suffice for a comparison of different areas. Because of the uncertain status of the hygrophilous species, they will not be taken in consideration. Sixteen forest-dependent species and twelve savanna and woodland species were recorded at Amani during the research period. The "savanna effect" therefore is 42%. Of course such a number is influenced by the intensity and duration of the study. A number of species known from the research area – even some endemics – were not recorded. Species with adults in the long dry season, or of low abundance are also underrepresented. The number can therefore only be an estimation.

Species of forest edges are less endangered by deforestation than species of clearings and dense forest. Especially forest ground species, like *Loveridgacris impotens* or *Ixalidium transiens*, can be regarded as indicators for intact forests (concerning density of the canopy, but not tree species composition). Changes in their distribution at Amani can be regarded as a result of changing land use and deforestation. An example for a site which might soon lose its naturally occurring grasshopper fauna is W2 (path through cultivation from Amani to Mbomole). This site still has some small forest patches left, where *Aresceutica subnuda*, *Rhainopomma usambaricum*, *Parepistaurus pygmaeus* and *Afrophlaeoba usambarica* are found. After deforestation the first two species will probably disappear, followed later by the others. During the survey period the savanna effect for this site was already higher (60%) than in the whole study area. It is likely that it will rise even more due to the loss of forest edge species and immigration of savanna species. The following section will deal with the typical factors causing variation in the composition of grasshopper communities and compare the savanna effect for the different habitat types.

Forest sites: Forests are characterized by low daytime temperatures and high humidity. The climatic variation is less than in open habitats (Iversen 1991b), and the vegetation structure is more complicated. Species occur in all strata from the canopy to the forest floor (Jago 1973). Uvarov (1977) mentions a scarcity of acridoids inside the forest. They are more confined to paths and clearings, which offer a warmer microclimate than dense forest (Jago 1973). Forest species usually have abnormally large compound eyes (*Rhainopomma usambaricum*) and long antennae (*Physocrobylus tessa*). Many seem to be nocturnal (Uvarov 1977). Auditory organs are often reduced or absent (Lentulidae, Eumastacoidea). This reduction is correlated with the loss of tegmina (Jago 1973). In forests, herbage may be missing or its growth can be dense and high; ferns and herbs are dominant. None of the forest species inhabits open habitats. In disturbed parts of the forest, species of open woodland (*Phaeocatantops femoratus*) may occur. The savanna effect in forests is low, though rises with disturbance (e. g., deforestation for cardamom cultivation) and opening of the canopy (Site M 0%, Site H 10%).

Forest edge sites: Temperature and humidity at the edge of a forest vary more than in the interior. Plant growth is usually dense grasses and herbs. The species communities are dominated by species of herbs

TABLE 1. Ecological groups of grasshoppers recorded from Amani.

Species	Ecological groups	Main habitat
Euschmidtia uvarovi *Mastarammea karazeki* *Stenoschmidtia elegans*	arboricolous and phytophilous forest species	forest species
Loveridgacris impotens *Ixalidium usambaricum*	ground-dwelling forest species	forest species
Rhainopomma usambaricum *Aresceutica subnuda* *Eupropacris pompalis* *Physocrobylus tessa* *Parodontomelus arachniformis* *Plagiotriptus carli*	phytophilous species of clearings and forest edges	forest species
Parepistaurus pygmaeus *Afrophlaeoba usambarica* *Gymnobothroides pullus*	species of open forest edges (and road edges)	forest species
Heteracris coerulipes *Eupropacris ornata*	species of insolated shrub	forest species
Acanthacris ruficornis *Oraistes luridus*	phyto-arboricolous woodland / savanna species	woodland and savanna species
Zonocerus elegans *Catantops melanostictus* *Phaeocatantops femoratus*	herbicolous woodland and savanna species	woodland and savanna species
Metaxymecus gracilipes *Acrida sulphuripennis* *Afroxyrrhepes procera* *Humbe tenuicornis*	graminicolous woodland and savanna species	woodland and savanna species
Trilophidia conturbata *Heteropternis couloniana* *Morphacris fasciata*	terricolous woodland and savanna species	woodland and savanna species
Oxya hyla *Atractomorpha acutipennis*	hygrophilous species	hygrophilous species

and bushes (*Eupropacris ornata*). Forb-feeding species (*Parepistaurus pygmaeus*) are present as well as grass-feeders (*Afrophlaeoba usambaricum*). The existence of a grasshopper species endemic to the East Usambaras, and preferring grassy patches, suggests grassland may have existed there for a long time. This is confirmed by early descriptions of the vegetation for the top of Mbomole hill (Site G) by Engler (1903). At this site today the vegetation differs considerably from Engler's description. *Lantana camara* has become abundant and has overgrown much of the former grassy habitat. During this research, *Afrophlaeoba usambarica* was still present at this site, but only on grassy patches. Ground-dwellers are missing, though occasionally immigrate from the forest. Species communities at forest edges may also contain woodland species (*Oraistes luridus*). The savanna effect is therefore higher than inside the forest (Site G 25%).

Cultivated sites: In cultivations, temperatures are the highest in the East Usambaras. During the day the humidity is much lower than in the forest interior. Apart from the cultivated crops, herbs and grasses dominate, but growth is sparse and open soil patches are common. Exceptions are cultivations on moist soils, where *Colocasia esculenta* is cultivated. Bushes and trees may or may not be present. Cultivated areas are dominated by terricolous savanna species (*Heteropternis couloniana*). Bush-dwelling (*Acanthacris ruficornis*) and phytophilous species (*Catantops melanostictus*) may occur as well. The savanna effect is highest in cultivations. This is particularly true for tea plantations, which are usually treeless and poor in herbs (Site V 71%, Site T 100%).

Lawn: Grasshoppers occur only sparsely on the lawn in the center of Amani. The temperature is much higher than in forest during daytime, the humidity lower. It is dominated by grasses. Graminivorous savanna species (*Acrida sulphuripennis*) occur. However, forest edge species (*Afrophlaeoba usambarica*) may be present where trees grow. Site ST is a mixture of forest edge and lawn. The savanna effect is therefore only 36%.

Road sites: Roads represent a broad variety of habitat types, from forested areas to open grassland. The temperature is higher than inside the forest; the vegetation density rises towards the road edges. Grasses and herbs are dominant. Terricolous savanna species (*Trilophidia conturbata*) occur where vegetation growth is sparse. In dense vegetation, phytophilous savanna species (*Catantops melanostictus*) and forest edge species (*Gymnobothroides pullus*) may be present, depending on the presence of trees. Both grass-feeders (*Afrophlaeoba usambarica*) and forb-feeders (*Rhainopomma usambaricum*) can be found. Roads through the forest can be regarded as ecological channels for savanna species (Uvarov 1977). The savanna effect is usually high (Site R 73%).

Swamp: The swamp is a humid but hot area, where vegetation-growth is dense and high. There are only scattered trees. Grasses dominate, but herbs are also common. The site is shaded in the evening by adjacent forest. This results in a composition of forest species, forest edge species, thicket species and hygrophilous species. Ground-dwellers and xerophilous species are absent. The high humidity is the main cause for the low savanna effect (Site B 13%).

Comparison with Mount Mlinga

The easternmost mountain ridge of the East Usambaras, Mount Mlinga, was visited only twice. The number of records is therefore much lower than at Amani. It is worth noting that despite of this, 25 species were recorded from Mlinga. As at Amani, they can be arranged into ecological groups (Table 2).

The savanna effect at Mt. Mlinga is much higher than at Amani (63%). According to Iversen (1991a), Mt. Mlinga was densely forested at the beginning of the century. At present only small disturbed forest patches remain. The mountain ridge is dominated by an oilpalm plantation. The species list from Mlinga is naturally far from complete. Arboricolous species were not recorded due to the short duration of the visits. Species with adults only in the long dry season were also not found. Nevertheless, the high number of savanna species is apparent. In Amani, some of the species common at Mt. Mlinga were not recorded or were rare. This might be explained by the milder climate and the higher degree of disturbance at the latter place. The forests are open-canopied, some are cultivated with cardamom. A typical grasshopper species of such a disturbed type of forest is *Phaeocatantops femoratus*.

Four factors are important when comparing the two species lists: the short survey duration at Mt. Mlinga, the different type of land-use (oilpalm plantation), the warmer climate and the high level of disturbance of the small forest patches.

Forest species: Species recorded from Amani by single specimens were not recorded from Mlinga, probably because of the short investigation period (this also increases the savanna effect). An interesting difference is the occurrence of two different species of *Ixalidium*,

with *I. usambaricum* in the forests of Mt. Mlinga (which have a lowland facies) and *I. transiens* in the submontane forests at Amani. This might be due to the warmer climate at Mt. Mlinga (*I. usambaricum* also occurs at the coast). Only two specimens of *I. usambaricum* were found, probably as a result of the high degree of disturbance of the Mt. Mlinga forests.

Species of clearings and forest edges: These ecological groups show greater similarities. *Eupropacris pompalis* was not recorded at Mt. Mlinga, probably because of its late seasonal occurrence. It is known from Mlingano and therefore not restricted to the submontane part of the East Usambaras. *Physocrobylus tessa* was recorded at Amani only sparsely. It therefore might be present also at Mt. Mlinga. It is obvious that species of open forest edges are normally more abundant than forest species.

Species of insolated shrubs: Neither of these species was recorded from Mt. Mlinga. Both are distributed throughout lowland and submontane forests in Tanzania and probably need high humidity. They therefore belong to the typical fauna of the East Usambaras. It is possible that *Heteracris coerulipes* was overlooked. *Eupropacris ornata* becomes adult in October and therefore could not have been recorded during the two visits at Mlinga in July and August.

Hygrophilous species: The occurrence of *Oxya hyla* and *Atractomorpha acutipennis* is mainly explained by the presence of moist soil with dense vegetation. *A. acutipennis* does not seem to be as hygrophilous as *O. hyla*. It is also present on the lake shore at Mlinga, where *O. hyla* is absent.

Savanna and Woodland species: Considering that *Zonocerus elegans* becomes adult in October, and that *Afroxyrrhepes procera* was recorded by only one specimen from Amani, the diversity and abundance of savanna species are much higher at Mt. Mlinga. Ten species occurred more commonly at Mt. Mlinga than

TABLE 2. Ecological groups of grasshoppers recorded from Mt. Mlinga.

Species	Ecological groups	Main habitat
Loveridgacris impotens	ground-dwelling forest species	forest species
Ixalidium usambaricum		
Rhainopomma usambaricum	species of clearings and forest edges	
Aresceutica subnuda		
Parodontomelus arachniformis		
Plagiotriptus carli		
Parepistaurus pygmaeus	species of open forest edges (and road edges)	
Afrophlaeoba usambarica		
Gymnobothroides pullus		
Acanthacris ruficornis	phyto-arboricolous woodland and savanna species	
Oraistes luridus		
Abisares viridipennis		
Taramassus cunctator	herbicolous woodland and savanna species	woodland and savanna species
Oxyaeida poultoni		
Phaeocatantops femoratus		
Catantops melanostictus		
Metaxymecus gracilipes	graminicolous woodland and savanna species	
Acrida sulphuripennis		
Protanita longiceps		
Humbe tenuicornis		
Trilophidia conturbata	terricolous woodland and savanna species	
Heteropternis couloniana		
Morphacris fasciata		
Chrotogonus hemipterus		
Atractomorpha acutipennis	hygrophilous species	hygrophilous species

TABLE 3. Comparison of species recorded from Amani and Mt. Mlinga (1: single specimen, 2: occasional occurrence (< 10 specimens), 3: dispersed occurrence, 4: common).

Species	Amani	Mt. Mlinga	Ecological group
Euschmidtia uvarovi	1		arboricolous and phytophilous forest species
Mastarammea karaseki	1		
Stenoschmidtia elegans	2		
Loveridgacris impotens	2	2	ground-dwelling forest species
Ixalidium transiens	3		
Ixalidium usambaricum		2	
Rhainopomma usambaricum	4	4	species of clearings and forest edges
Aresceutica subnuda	4	3	
Eupropacris pompalis	4		
Physocrobylus tessa	2		
Parodontomelus arachniformis	3	3	
Plagiotriptus carli	1	2	
Parepistaurus pygmaeus	4	4	species of open forest edges (and road edges)
Afrophlaeoba usambarica	4	3	
Gymnobothroides pullus	4	4	
Heteracris coerulipes	3		species of insolated shrub
Eupropacris ornata	4		
Acanthacris ruficornis	2	2	phyto-arboricolous woodland and savanna species
Oraistes luridus	2	3	
Abisares viridipennis		2	
Taramassus cunctator		3	herbicolous woodland and savanna species
Oxyaeida poultoni		3	
Catantops melanostictus	3	4	
Zonocerus elegans	2		
Phaeocatantops femoratus	2	4	
Metaxymecus gracilipes	2	3	graminicolous woodland and savanna species
Acrida sulphuripennis	2	3	
Afroxyrrhepes procera	1		
Protanita longiceps		3	
Humbe tenuicornis	2	2	
Chrotogonus hemipterus		2	terricolous woodland and savanna species
Trilophidia conturbata	4	4	
Heteropternis couloniana	4	4	
Morphacris fasciata	3	4	
Atractomorpha acutipennis	4	4	hygrophilous species
Oxya hyla	4		

at Amani, and none was more common at Amani. Some species were only recorded from Mlinga, although the survey period was much longer at Amani. *Taramassus cunctator* and *Chrotogonus hemipterus* have been already recorded from Amani (Kevan 1959), but *Oxyaeida poultoni*, *Protanita longiceps* and *Abisares viridipennis* do not seem to occur here. The higher abundance of savanna species at Mt. Mlinga causes a higher savanna effect. This can be explained by two factors: the warmer climate, allowing more thermophilous species to develop, and the smaller and more disturbed patches of forest left at Mlinga, giving savanna species larger areas for dispersal.

The different abundance of savanna and woodland species at cultivations in Amani and Magrotto (Mt. Mlinga) are probably the result of the cooler

Amani		climatic tolerance	Mt. Mlinga	
frequency	species		species	frequency
4	*Trilophidia conturbata*	1	*Trilophidia conturbata*	4
4	*Heteropternis couloniana*	1	*Heteropternis couloniana*	4
3	*Catantops melanostictus*	2	*Catantops melanostictus*	4
3	*Morphacris fasciata*	2	*Morphacris fasciata*	4
2	*Phaeocatantops femoratus*	3	*Phaeocatantops femoratus*	4
2	*Metaxymecus gracilipes*	4	*Metaxymecus gracilipes*	3
2	*Acrida sulphuripennis*	4	*Acrida sulphuripennis*	3
2	*Oraistes luridus*	4	*Oraistes luridus*	3
		6	*Protanita longiceps*	3
		6	*Oxyaeida poultoni*	3
		6	*Taramassus cunctator*	3
		6	*Abisares viridipennis*	2
		6	*Chrotogonus hemipterus*	2
2	*Humbe tenuicornis*	5	*Humbe tenuicornis*	2
2	*Acanthacris ruficornis*	5	*Acanthacris ruficornis*	2

FIG. 6. Climatic tolerance of savanna species in the east Usambaras according to their estimated frequency at Amani and Mt. Mlinga.

climate and higher humidity at Amani. It is possible to put the species in a sequence according to their abundance at open places at Amani and Mt. Mlinga, so that their climatic tolerance becomes clear (Fig. 6). Species with greater abundance at high altitudes are here regarded as having a higher climatic tolerance. *Zonocerus elegans* and *Afroxyrrhepes procera* are not taken into consideration, because the former could not have been recorded from Mlinga due to its late adult emergence and only a single specimen of the latter was found at Amani. The climatic preferences of grasshoppers can be explained by the direct influence of temperature and water on the development of eggs, nymphs and adults (Uvarov 1966). Since water content of the soil does not seem to be a limiting factor in the East Usambaras, it seems that egg and nymph development are highly dependent on temperature. For several savanna species the temperature at higher altitudes might be too low for development (Uvarov 1966).

ACKNOWLEDGEMENTS

This research would not have been possible without the help of many people. I especially wish to thank Dr. Alan Tye, the conservation advisor of the East Usambara Conservation and Development project. He was very helpful during the organization and research periods. I also want to thank my local contact, Prof. Kim Howell for his advice. I am grateful to Prof. Dr. Dietrich Mossakowski, who organized the funding of this research, and Dr. Hakon Nettmann for his involvement. Prof. Dr. Gerhard Schmidt gave me much advice during the organization of the research. I want to express my thanks to Dr. Herbert Hohmann, Heinrich Kuhbier, Helmut Riemann and Georg Lakmann, who allowed me to study the grasshopper collection of the Überseemuseum Bremen. Dr. Niels Kristensen and Dr. Henrik Enghoff invited me to study the collection of the Zoological Museum in Copenhagen. I am indebted to Dr. Nicholas D. Jago, Dr. J. Mark Ritchie and Dr. Stuart Green, who helped me to identify the grasshoppers at the NRI in Chatham. They also gave me a great deal of useful information on some genera which are in process of revision by the NRI. Special thanks are due to my parents Walter and Heike Hochkirch, who gave me financial support during my studies in Germany and Tanzania, and visited me there. I am much obliged to Tessa Lachmund, Andrea Franke, Ralf Bischoff and Detlev Kelm for their companionship and help during the study. I also want to thank Dr. Julius Ningu, the project manager of the East Usambara Conservation and Development project, for free accommodation at the IUCN-resthouse and his information on regional conservation problems. In this connection I also have to thank Yusufu Mikidadi, Matilda Joseph, Halima Saidi and Magreth Dismas

for their perfect hospitality during my time at Amani, and Julian for the accommodation and food at Magrotto. My deep gratitude goes to the IUCN staff, especially Preben Enghard and Graham, who helped me during any problems at Amani. I also wish to thank Laura Watson, Tom Evans and Anna Baker for their companionship. Andrea Gottlieb very kindly corrected the manuscript. Finally, I wish to express my thanks to the Commission for Science and Technology (COSTECH) for giving me the research clearance for this study.

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