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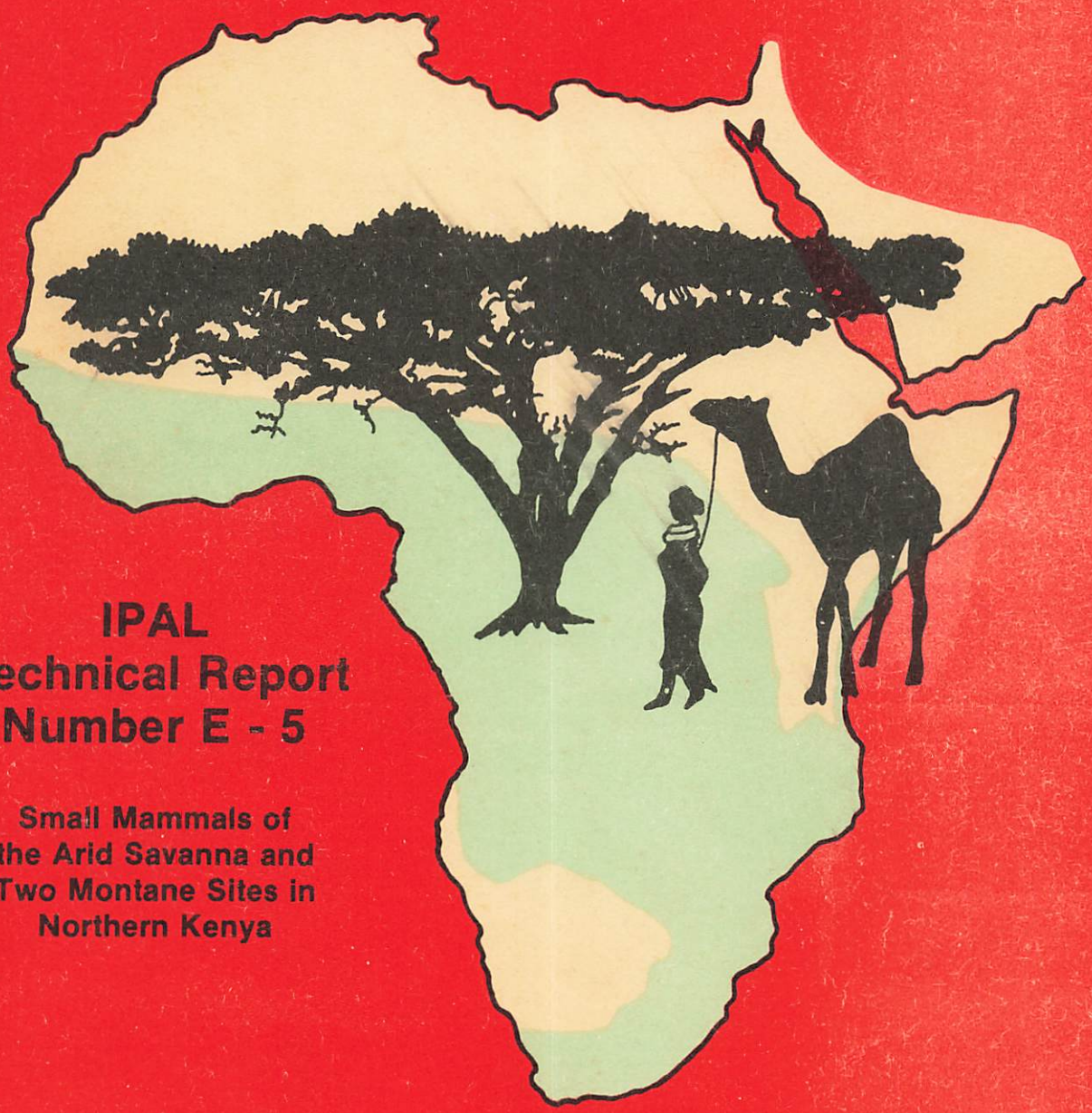


IPAL Technical Report Number E - 5

Small Mammals of the Arid Savanna and Two Montane Sites in Northern Kenya

MAN AND THE BIOSPHERE PROGRAMME

Project 3: Impact of Human Activities and Land Use Practices on Grazing Lands

IPAL Technical Report Number E - 5

SMALL MAMMALS OF THE ARID SAVANNA AND TWO MONTANE SITES IN NORTHERN KENYA

by

G. H. G. Martin,

J. J. Opiyo

P. Simpkin,

SOME ACRIDIDS OF ARID AND SEMI-ARID SOUTHWESTERN MARSABIT DISTRICT, NORTHERN KENYA

by

R. O. Okelo

October 1981

UNEP-MAB Integrated Project in Arid Lands

SUMMARY INTRODUCTION TO IPAL AND THE TECHNICAL REPORT SERIES

The Integrated Project in Arid Lands (IPAL) was established by UNESCO with financial support from UNEP in 1976 with the aim of finding direct solutions to the most urgent environmental problems associated with desert encroachment and ecological degradation of arid lands. It forms part of the international UNESCO programme, Man and the Biosphere (MAB) which has links not only with UNEP's Desertification Unit but also with FAO, in response to the Plan of Action adopted by the 1977 United Nations Conference on Desertification. It is an example of the type of pilot activity that UNESCO and UNEP, together with other organizations and a number of governments, are trying to promote to provide the scientific basis for the rehabilitation and rational management of arid and semi-arid zone ecosystems, through integrated programmes of research (including survey, observation and experimentation), training and demonstration. Phase III of the project, 1980-1983, is supported by funds in trust to UNESCO provided by the Federal Republic of Germany.

During the first phases of IPAL, a co-ordination unit was established in Nairobi and the initial field work started in the arid zone of northern Kenya in a working area of 22,500 km^2 situated between Lake Turkana and Marsabit Mountain. The project now operates five field stations at Mount Kulal, Olturot, Kargi, Korr and Ngurunit, with the project headquarters in Marsabit which is the administrative centre of the District. Since its establishment the project has researched several aspects of experimental management of the region, concentrating upon 'human ecology' of the nomadic pastoralists in dynamic inter-relationship with the animals, plants and the other resources of a drought-prone, uncertain environment.

During the next three years (1980-1983), the investigations in progress will be extended and intensified to develop resource management plans of models for the area, taking into account the increasing human population, the trend towards sedentarization, the degradation of primary productivity, and the increasing incidence of soil erosion, all of which are factors resulting in the necessity of constant famine relief measures in this region. Results obtained in the project are the subject of a number of training workshops and seminars in which Kenyan and regional scientists from the Sudano-Sahelian region participate.

This report is one of a series published by IPAL describing technical findings of the Project and, where appropriate, giving management recommendations relating to the central problems of ecological degradation in the arid zone. The reports are divided into the following categories distinguished by the base colours of their covers:

A. general, introductory and historical: white

B. climate and hydrology: blue

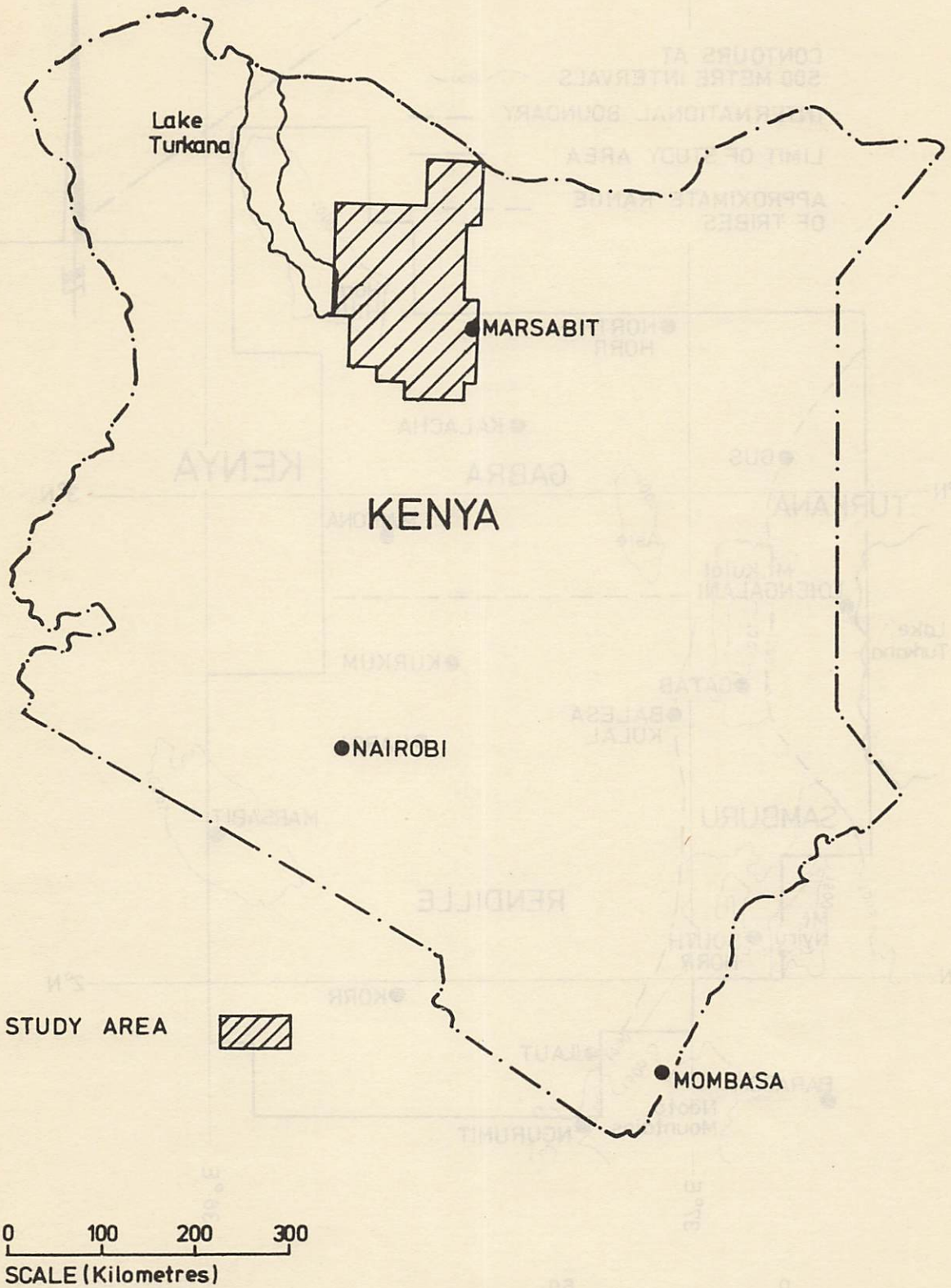
C. geology, geomorphology and soils: brown

D. vegetation: green

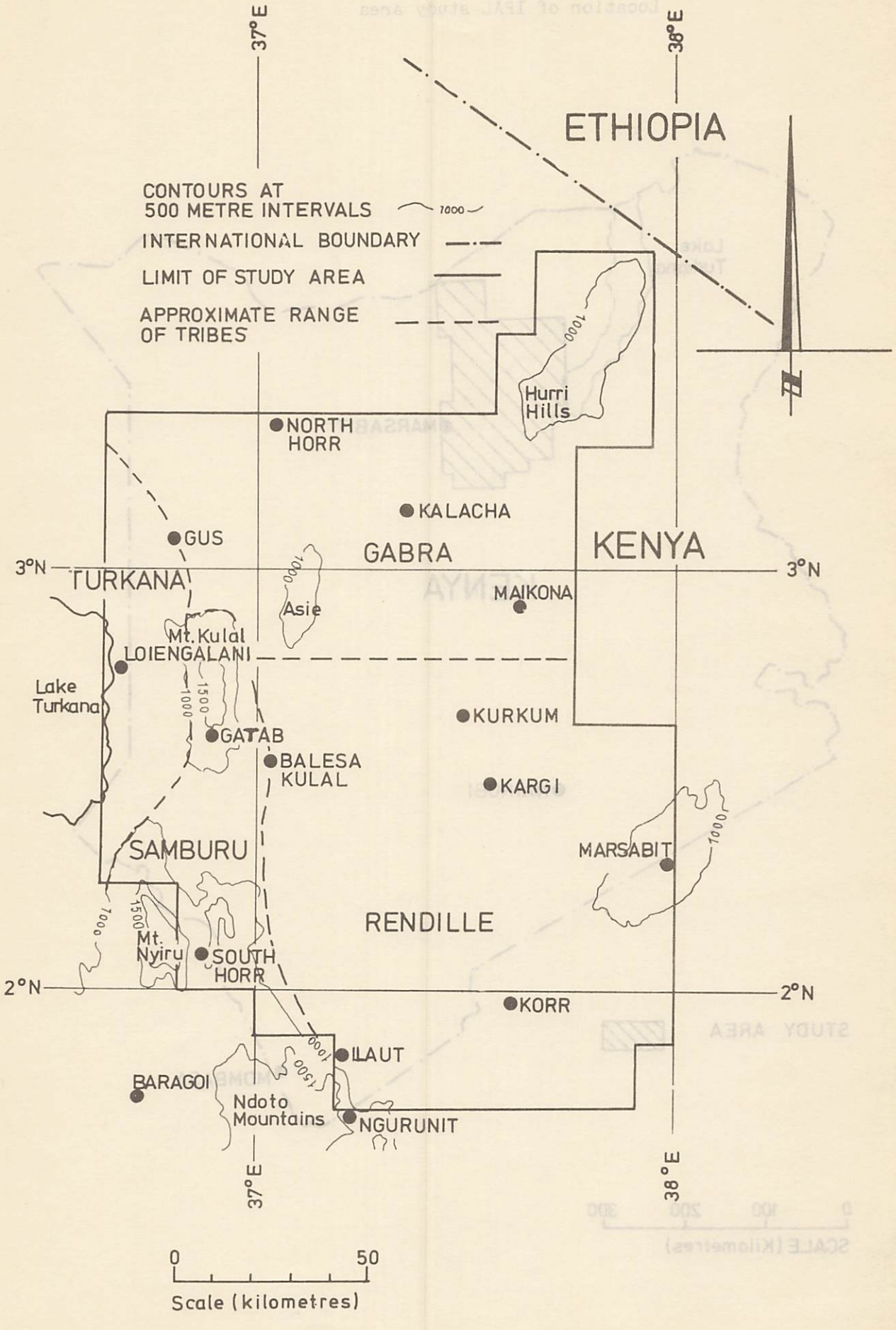
E. livestock and other animal life: red

F. social and anthropological : yellow.

Location of IPAL study area



The study area



SMALL MAMMALS OF THE ARID SAVANNA AND TWO MONTANE SITES IN NORTHERN KENYA

by
G.H.G. Martin
J.J. Opiyo

Department of Zoology
Kenyatta University College, Nairobi

P. Simpkin

Department of Environmental Science
Westfield College, United Kingdom

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SMALL MAMMALS OF THE ARID SAVANNA AND TWO MONTANE SITES IN NORTHERN KENYA

G. H. G. Martin, J. J. Opiyo and P. Simpkin

1. Summary

A report is given on field studies of small mammals in the Mt. Kulal region of northern Kenya during 1979 and 1980.

In 4478 trap-days six species of rodents were recorded from eight arid habitats studied and three species from two montane sites.

The results from the current study are compared with previous work in the area. Discussion is made of possible reasons for the generally low trapping success and the apparently impoverished small mammal fauna of Mt. Kulal.

2. Introduction

A large part of northern Kenya is arid land merging into semi-desert. It thus falls into eco-climatic zones V and VI described by Pratt and Gwynne (1977). The region is of particular importance as it is a zone of increasing desertification and is a study area of the UNEP-MAB Integrated Project in Arid Lands (IPAL).

Project scientists are conducting programmes of applied research into the ecology of the area. Studies have been made or are in progress on the relationship between man, livestock and the environment as well as projects investigating the climate, vegetation, geology and aspects of the ecology of wild animals.

Little is known about small mammals in the various habitats in the area. This paper describes two pilot field studies aimed at increasing knowledge of the role of these animals in local ecosystems.

The first study was a six-week undergraduate project carried out in July and August 1979 by Opiyo. The field data and material returned to the laboratory were analysed by Martin.

The second study was made in three weeks in July 1980 by Martin and Simpkin.

3. The general study area and environmental factors

3.1 Location

The study area lies between the southeastern shore of Lake Turkana and Marsabit Mountain in northern Kenya. Access from Nairobi is either from Marsabit in the west or via Maralal and South Horr from the south.

3.2 Topography and soil

Soil and geomorphological maps of the study area are being prepared by Dr P. M. Sinda at the IPAL research station at Gatab, Mt. Kulal.

Most of the area consists of a large 'desert' plain surrounded by hills of volcanic origin: Mt. Kulal (2295m) in the west, Mt. Marsabit (1930m) in the east, the Hurri Hills (1310m) to the north and the Nyiru and Ndoto Mountains to the south. Soils are derived from two parent materials, Precambrian basement rocks or recent volcanics.

3.3 Climate

Edwards et al. (1979) have made the most pertinent, although preliminary, analysis of climatological data from the area. Rainfall is usually low, highly variable and of short duration. The main rains occur in two seasons, March to May and October to December. Most of the area has less than 200mm of rain a year.

At higher altitudes, rainfall amount and duration increases while variability decreases. At Gatab, on Mount Kulal, rainfall is about 600mm a year and higher up it exceeds 900mm. Potential evaporation over most of the region is high and has been estimated at 2620mm per annum (FAO,1971).

3.4 Vegetation

Herlocker (1979) has prepared the most recent study of the vegetation of the study area.

Nine primary physiognomic vegetation types can be recognized. These have been further sub-divided into 73 tertiary vegetation types. The primary physiognomy ranges from annual grassland to evergreen mountain forest. The three principal vegetation types, in order of area covered, are annual grassland, dwarf shrubland and shrubland. All three occupy the drier part of the environmental gradient within the study area.

4. 1979 field study in the Balessa Kulal and Kargi areas

4.1 Habitats studied

4.1.1 Riverine Acacia

4.1.1.1 Riverine Acacia. The site was adjacent to the IPAL exclosures. The sandy soil had a good vegetation cover with a mixture of *Acacia tortilis*, *Acacia reficiens* and *Acacia nubica* over a layer of *Duosperma eremophilum* and grasses that include *Aristida mutabilis*, *Cenchrus* sp. *Chloris roxburghiana*.

4.1.1.2 *Acacia reficiens* shrubland. This shrubland was about a kilometre south of the IPAL rondaval on the north side of of the Balessa Kulal river. The fine sandy soil supported the dominant *Acacia reficiens* with scattered specimens of *Acacia nubica* and *Commiphora africana* over an understorey of *Indigofera spinosa* and the grass *Chloris roxburghiana*.

4.1.1.3 Old lava flow. Adjacent and southeast of the rondaval was an area of lava rocks with little ground cover and scattered specimens of *Acacia reficiens*, *Acacia tortilis* and *Commiphora africana*.

4.1.2 Kargi (altitude 533m)

4.1.2.1 Lava field. This degraded habitat near the centre of Kargi supported occasional stunted *Terminalia orbicularis* and a less than 10% cover of the grass *Chrysopogon aucheri*.

4.1.2.2 Lava outcrop. South of Kargi was an area of sandy soil with extensive areas of exposed lava rocks. *Jatropha* sp. was the dominant shrub in this area.

4.1.2.3 Low sand dunes. To the east of Kargi was an area of low sand dunes with a sparse vegetation cover of occasional specimens of *Cadaba farinosa*. *Capparis tomentosa* and *Cleome* sp. Grasses recorded were *Chrysopogon aucheri*, *Aristida adscensionis*, *A. mutabilis* and *Dactyloctenium* sp.

4.2 Methods

Metal snap traps and Sherman live traps were used to trap the small mammals.

In each of the six habitats, the live traps were laid in a square grid with a 30-metre trap interval. The effective trapping area was estimated at approximately 6.0 hectares. The trapping area was calculated by adding the area of the 35-metres wide boundary strip to the area of the grid. A boundary strip makes allowances for the range of animals caught at the edge of the grid. It has been suggested that the width of the boundary strip should be the average distance travelled in between successive captures of animals caught five times or more (Fleming, 1971). However, so few animals were recaptured that this measurement could not be made, so a somewhat arbitrary figure of 35-metres was used. This figure was about that calculated for the widest ranging rodent species by Cheeseman and Delany (1979) in a thick grassland savannah area. It is probable that the 35-metre figure is a low estimate for the more arid conditions of the present study area.

The snap traps were laid in a line in an area adjacent to the live trap grid.

Each site was trapped for six days and traps were inspected twice a day between 0615 hours and 0800 hours and between 1730 hours and 1830 hours.

The principal bait used was peanut butter, but maize meal and grain, sugar cane and mixtures of some or all of these were tried at various times.

4.3 Results

Six of the eleven sites are examples of some of the mosaic of habitats found in the arid savanna area of the southwest Marsabit District and are therefore considered together.

4.3.1 Trap success rates

Six species of small mammals were trapped during the course of the study: five rodent species, *Tatera nigricauda*, *Gerbillus gerbillus*, *Arvicanthis nilotica*, *Acomys subspinosus* and *Xerus rutilans*; and one insectivore, *Elephantulus refescans*. An overall trap success of 4.1% was achieved, 95 animals being caught in 2343 trap days (Table 1).

Snap traps proved to be up to five times more effective than live traps with an overall success rate of 9.7% compared to 1.9% . However, it should be noted that snap traps were capable of catching species larger than those normally caught in the live traps. It is unlikely that a box trap of the Sherman type measuring 230 x 75 x 90 mm would often catch a species as large as the ground squirrel, *Xerus rutlians*, which has a head and body measurement ranging from 200 - 255mm (Kingdon, 1975). In fact no specimen of *Xerus* was caught in a live trap.

If the number of *Xerus* caught is deducted from the total catch of the snap traps, the success rate drops to 8.0% - still four times that for live traps (Table 1).

Table 1
Trapping success in arid areas (1979)

Location and Habitat	Trap days			Number of Animals caught					Trap success %				
	Snap	Live	Total	Snap	Snap* -*Xerus*	Live	Total	Total* -*Xerus*	Snap	Snap* -*Xerus*	Live	Total	Total* -*Xerus*
Balessa Kulal													
Acacia reficiens	120	282	402	20	16	6	26	21	16.7	13.3	2.1	5.0	5.2
Riverine *Acacia*	120	282	402	15	15	5	20	20	12.5	12.5	1.8	5.0	5.0
Lava	118	282	400	8	5	6	14	11	6.8	4.2	2.1	3.5	2.8
TOTAL	358	846	1204	43	36	17	60	52	12.0	10.0	2.0	5.0	4.3
Kargi													
Degraded lava	106	282	388	3	1	2	5	3	2.8	0.9	0.7	1.3	0.8
Lava outcrop	88	282	370	15	13	13	28	26	17.0	14.8	4.6	7.6	7.0
Sand dune	99	282	311	2	2	0	2	2	2.0	2.0	0.0	0.5	0.6
TOTAL	293	846	1139	20	16	15	35	31	6.8	5.5	1.8	3.1	2.7
GRAND TOTAL	651	1692	2343	63	52	32	95	83	9.7	8.0	1.9	4.1	3.5

*Numbers of *Xerus* caught were subtracted from trap results to increase comparability of snap and live traps because live traps are unlikely to catch *Xerus* (See text for further information).

Combined snap and live trap success rate varied considerably between the six habitats ranging from 0.5% in the sand dune area at Kargi to 7.6% in the lava outcrop south of Kargi. Trap effectiveness between snap and live traps for each species is compared in Table 2. Only in the case of *Arvicanthis* was there no significant difference in the catch rate. In all other instances the difference in rate was marked.

4.3.2 Species distribution

The low numbers of individuals of the different species caught in the six habitats studied make it difficult to draw reliable conclusions about species distribution (Table 3). For example there was no obvious reason why *Tatera* and *Xerus* should not be found in the riverine area at Balessa Kulal.

Nevertheless, it is worth noting that in 2343 trap-days, *Acomys* was only recorded from the old lava area at Kargi, where it was relatively abundant, and *Elephantulus* was only found in the *Acacia reficiens* area at Balessa Kulal. *Gerbillus* was the only species recorded from the sand dune area at Kargi. *Xerus* was the most widespread species being found in four out of the six habitats studied.

Trap success rate, i.e. the number of species and individuals caught in the habitats, can act as crude indications of habitat richness. These data are tabulated in Table 4.

It is clear that the degraded lava and sand dune sites at Kargi were the poorest sites for small mammals. The relatively high success rate and large number of individuals recorded at the lava outcrop south of Kargi is almost entirely due to the large number of specimens of one species, *Acomys*, caught at this site - 23 of a total of 26 individuals captured.

On all other counts, the habitats at Balessa Kulal appeared to be more favourable for small mammals.

Table 2
Trap effectiveness (%) for different species (1979)

Gerbillus		*Tatera*		*Arvicanthis*		*Acomys*		*Xerus*		*Elephantulus*	
Snap	Live	Snap	Live	Snap	Live	Snap	Live	Snap	Live	Snap	Live
4.7	0.6	6.3	0.9	1.2	0.9	4.8	4.6	2.55	-	3.3	0.7
+		+		-		+		+		+	

+ significant $P \leq 0.5$ - not significant

Table 3
Numbers of individuals of each species caught in each habitat (1979)

Habitat	Trap type	No. spp. caught	*Tatera*	*Gerbillus*	*Avicanthis*	*Acomys*	*Xerus*	*Elephantulus*	Total
Balessa Kulal									
Acacia reficiens	Snap	4	10	2	0	0	4	4	20
	Live	3	2	1	0	0	0	1	4
	Combined	4	12	3	0	0	4	5	24
Riverine *acacia*	Snap	2	0	12	3	0	0	0	15
	Live	2	0	3	1	0	0	0	4
	Combined	2	0	15	4	0	0	0	19
Lava	Snap	2	5	0	0	0	3	0	8
	Live	2	1	0	2	0	0	0	3
	Combined	3	6	0	2	0	3	0	11
Kargi									
Degraded lava	Snap	2	0	0	1	0	2	0	3
	Live	1	0	0	2	0	0	0	2
	Combined	2	0	0	3	0	2	0	5
Lava outcrop	Snap	2	0	0	0	13	2	0	15
	Live	1	0	0	0	9	0	0	9
	Combined	2	0	0	0	22	2	0	24
Sand dune	Snap	1	0	2	0	0	0	0	2
	Live	0	0	0	0	0	0	0	0
	Combined	1	0	2	0	0	0	0	2
	TOTALS		18	20	9	22	11	5	

Table 4

Trap success, numbers of individuals and species caught, used as crude indicators of habitat richness(1979)

Habitat	Trap success%	No. species caught	No. individuals caught
Balessa Kulal			
Acacia reficiens	6.5	4	24
Riverine *acacia*	5.0	2	19
Lava	3.5	3	11
Kargi			
Degraded lava	1.7	2	5
Lava outcrop	7.6	2	26
Sand dune	0.5	1	2

4.3.3 Daily activity patterns

The results of morning and evening catches are presented in Table 5. The data are insufficient to draw conclusions about *Elephantulus* but the difference in morning and evening catches are significantly different in the other species. *Aerus* is diurnal whereas *Tatera*, *Gerbillus*, *Arvicanthis* and *Acomys* are nocturnal or crepuscular species.

4.3.4 Density estimates

The effective trapping area of the live trap grid was estimated at 6.0 hectares. The number of individuals trapped on a grid using live traps ranged from nil on the sand dune area at Kargi to nine from the lava outcrops south of Kargi (Table 3). The average number of individuals trapped on a grid was 3.7 (Table 6). No animal was captured more than twice, thus accurate estimates of density could not be made.

Minimum estimates can be made using numbers of individuals trapped on a grid (Table 6). Such estimates would range from 0/ha on the Kargi sand dunes (a known underestimate as two *Gerbillus* were caught by snap traps in the area; Table 3) to 1.5/ha on the Kargi lava outcrops. Even assuming a fourfold increase suggested by snap trap success rates, densities appear to be of the order of two or three small mammals a hectare. The presence of trap-shy animals in the grid area would increase these figures, but it is likely that the order of magnitude would be much the same.

The effective trapping area may be too low an estimate because although there were inadequate numbers of recaptures to make realistic estimates, the data in Table 7 suggest the average distance between successive captures would be in excess of the 35 metres used to calculate the width of the boundary strip.

If the average distance between captures is close to these estimates then, of course, density estimates would be correspondingly reduced.

Table 5.
Daily activity patterns based on catches (1979)

	Morning catch (nocturnal/crespuscular activity)	Evening catch (diurnal activity)
Tatera	16	4
Gerbillus	21	0
Avicanthis	9	2
Acomys	26	0
Xerus	0	11
Elephantulus	2	4

Table 6
Density estimates (1979)

Habitat	No. individuals caught	Effective grid area (ha)	Minimun No./ha based on live captures	No./ha assuming x4 underestimate of captures by live traps (*Xerus* not included)
Balessa Kulal				
Acacia reficiens	Snap 20			
	Live 4	6	0.7	2.8
Riverine *acacia*	Snap 15			
	Live 4	6	0.7	2.8
Lava	Snap 8			
	Live 3	6	0.5	2.0
Kargi				
Degraded lava	Snap 3			
	Live 2	6	0.3	1.2
Lava outcrop	Snap 15			
	Live 9	6	1.5	6.0
Sand dune	Snap 2			
	Live 0	6	0	0
			Av. 0.6	Av. 2.4

Table 7
Recapture distances of species caught at Balessa Kulal and Kargi

Species	Average recapture Distance (metres)	Comments
Tatera	120	Two individuals, each recaptured once
Gerbillus	120	One individual, recaptured once
Avicanthis	100	Two individuals, each recaptured once
Acomys	55	Four individuals, each recaptured once
Elephantulus	60	One individual, recaptured once
	Av. 84	

5. 1980 field studies at Ol Torot and Mt. Kulal

5.1 Habitats studied

5.1.1 Ol Torot (altitude 660m)

Both sites at Ol Torot were on the edge of a ground-water supplied *Acacia tortilis* woodland where it was merging into other vegetation types. The sites have, therefore, been named after the common shrub species present.

5.1.1.1 *Duosperma/Solanum* shrubland

The grid was laid out about 200 metres west of the IPAL manyatta in an area where *Duosperma* sp. and *Solanum* sp. were the dominant shrubs.

5.1.1.2 *Duosperma/Indigofera/Sisola* shrubland

This site was approximately 200 metres south of the airstrip. In the area specimens of the salt-indicating *Salvidora* sp. and *Sisola* sp. were common but the codominant shrubs were *Duosperma* and *Indigofera*.

5.1.2 Mt. Kulal (altitude 2000m)

Two habitats were studied. The sites were adjacent and located where the edge of the montane evergreen forest interdigitates with an area of perennial grassland about three kilometres north along the track from the IPAL research station at Gatab.

5.1.2.1 Perennial grassland

In this thickly grassed meadow three species of grass were codominant, *Themeda trianda*, *Setaria* sp. and *Sporobolus* sp.

5.1.2.2 Forest

The principal tree species in the area of the grid were *Olea hockstellari*, *Teclea simplicifolia* and occasional specimens of *Cassipourea malosane* and *Juniperus procerea*. The ground cover varied in density but over much of the area of the grid was quite sparse.

5.2 Methods

Snap traps and Sherman live traps were used. On both sites at Ol Torot an 8 x 8 live trap grid was laid. The trap interval in the *Duosperma/Solanum* area was fifteen metres whilst at the *Duosperma/Indigofera/Sisola* area traps were set at ten-metre intervals. Lines of snap traps were set adjacent to the two grids. Snap traps were also set above ground in bushes along a small lugga between the airstrip and *Duosperma/Indigofera/Sisola* trapping grid.

On Mt. Kulal, because it was thought that the forest might prove richer in species than the grassland, it was decided to concentrate a large proportion of our trapping effort in the forest. Therefore a 9 x 9 live trap grid was laid in the forest and a 4 x 10 grid placed in the grassland. A ten-metre trap interval was employed on both grids.

A line of snap traps at ten-metre intervals was set in three locations in the forest with ground and above-ground traps at each trap station. Two lines of snap traps were laid in the grassland. The above-ground traps at Ol Torot and Kulal were set between one and two metres above ground.

The effective trapping area of the live-trap grids was calculated using a 35-metre boundary strip. The effective trapping areas were thus:

- Ol Torot. 3.0 hectares *(Duosperma/Solanum* site) and 2.0 hectares *(Duosperma/Indigofera/Sisola* site).
- Mt. Kulal. 2.25 hectares (forest site) and 1.6 hectares (grassland site).

5.3 Results

The Ol Torot sites are near the boundary between eco-climatic zones V and VI - much the same as those examined during the 1979 study. They form further examples of the habitat mosaics of the arid land of the southwest Marsabit district. On the other hand, the Mt. Kulal sites are examples of forest and derived grassland habitats that comprise eco-climatic zone II of Pratt and Gwynne (1977).

It is therefore convenient for the purpose of comparison to consider the results from the Ol Torot and Mt. Kulal sites separately.

5.3.1 Ol Torot

5.3.1.1 Trap success rate. Three species of rodent were trapped in the ground traps at Ol Torot, *Tatera nigricauda*, *Acomys subspinosus* and *Gerbillus gerbillus*. A very low trap success rate with ground traps was achieved with an overall trap success rate of 0.9%, eight catches being made in 925 trap-days (Table 8). Live traps were three to four times more successful than snap traps and had a success rate of 1.1% compared to 0.3%. In the snap traps only one specimen, *Tatera nigicauda*, was caught in the *Duosperma/Solanum* area in 160 trap-days; no animals were caught in 125 trap-days in ground traps along the lugga adjacent to the *Duosperma/Indigofera/Sisola* grid.

There was little difference in the live trapping rate between the two habitats: 1.2% in the *Duosperma/Solanum* site and 0.9% in the *Duosperma/Indigofera/Sisola* area (Table 8).

5.3.1.2 Species distribution. Three individuals were recorded from the grid near the IPAL manyatta, two *Acomys subspinosus* and one *Tatera nigricauda* (recaptured once): on the grid south of the airstrip two individuals were caught, one *Tatera nigricauda* (recaptured once) and one *Gerbillus gerbillus* (Table 9).

Two specimens of *Graphiurus (Claviglis) murinus* was trapped in above ground traps near the *Duosperma/Indigofera/Sisola* site.

5.3.1.3 Daily activity patterns. All animals were caught under either nocturnal or crepuscular conditions.

Table 8
01 Torot trap success rates (1979)

Habitat	No. trap days			No. animals caught			Trap success %		
	Snap (above ground)	Snap (ground)	Live	Snap (above ground)	Snap (ground)	Live	Snap (above ground)	Snap (ground)	Live
Duosperma/ Solanum	0	160	320	0	1	4	-	0.3	1.30
Duosperma/ Indigofera/ Sisola	125	125	320	1	0	3	0.6	0	0.9
TOTALS	125	285	640	1	1	7	0.6	0.2	1.1

Table 9
Numbers of individuals caught at Ol Torot (1980)

Habitat	Trap type	No. species caught	*Gerbillus*	*Tatera*	*Acomys*	*Claviglis*	Total
Duosperma/ Solanum	Snap (ground)	1	0	1	0	0	1
	Live	2	0	1	2	0	3
Duosperma/ Indigofera/ Sisola	Snap (ground)	0	0	0	0	0	0
	Live	2	1	1	0	0	2
	Snap (above ground)	1	0	0	0	1	1

5.3.1.4 Density estimates. The numbers of animals capturedwere so low that density estimates cannot be realistically made, but the results suggest that rodent densities are very low, possibly of the order of one or two a hectare.

5.3.2 Mt. Kulal

5.3.2.1 Trap success rates. A total of three species of rodents, *Praomys (Myomyscus) fumatus*, *Thamnomys (Grammomys) dolichuris* and *Graphiuris (Claviglis) murinus*, and one unidentified shrew, were trapped at the Mt. Kulal sites. The grassland site had a live trap success rate of 5.4% with 13 catches in 240 trap-days, but no animals were caught in 100 trap-days in the snap traps (Table 10). In the forest, the live trap grid had only a single trap success in 446 trap days.

In 150 days of snap trapping on the ground, two animals were caught whilst in the above ground snap traps seven animals were caught in 149 trap-days (Table 10). Thus the succes rates in the forest were 0.2% for live traps, 1.3% for ground snap traps and 4.7% for above ground snap traps.

5.3.2.2 Species distribution. *Myomyacus* was the only rodent caught in the meadow. The capture of two individuals in the forest was possibly due to the close proximity of the trap line in which they were caught to the grassland area. A single *Claviglis* was caught in a live trap in the forest but all other specimens of both *Claviglis* and *Grammomys* were caught in above-ground situations in bushes, trees or on a cliff face in the forest (Table 11). The only shrews caught were found in the grassland area.

5.3.2.3 Daily activity patterns. No animals were caught during the day in either the forest or grassland sites.

5.3.2.4 Density estimates. Low catch rates make it impossible to make any accurate estimate of small mammal populations in either grassland or forest situations.

Table 10
Mount Kulal trap success rates (1980)

Habitat	No. trap days			No. animals caught			Trap success %		
	Snap (above ground)	Snap (ground)	Live	Snap (above ground)	Snap (ground)	Live	Snap (above ground)	Snap (ground)	Live
Grassland	0	100	240	0	0	13	-	0	5.4
Forest	149	150	446	7	2	1	4.7	1.3	0.2
TOTALS	149	250	686	7	2	14	4.7	0.8	2.0
		936			16			1.7	

Table 11
Numbers of individuals caught on Mount Kulal in (1980)

Habitat	Trap type	No. species caught	*Myomyscus*	*Grammomys*	*Claviglis*	Shrews	Total
Grassland	Live	2	8	0	0	2	10
	Snap	0	0	0	0	0	0
Forest	Snap (ground)	1	2	0	0	0	2
	Live	1	0	0	1	0	1
	Snap (above ground)	2	0	3	4	0	7

It may be worth noting, however, that in the forest one animal, that being the primarily aboreal *Claviglis*, was caught in a grid with an effective trapping area of 2.25 hectares. In contrast, on the meadow grid, with an effective trapping area of 1.6 hectares, eight individual rodents and two shrews were caught. Based on these data, minimum 'guestimates' of small mammal densities for ground-dwelling species would be of the order of less than one a hectare in the forest, and about six per hectare in the grassland.

5.3.2.5 Breeding data. Six female *Myomyscus* were captured live and of these three were pregnant. Two female *Myomyscus* snap trapped near the forest edge and both had a uterus that was wide and vascular.

6. Discussion

6.1 Small mammals recorded from the Mt. Kulal region

The variety of species recorded during the current studies is similar to that found by the Royal Geographical Society expeditions to South Turkana (Coe, 1972). The report on the expeditions of 1968, 1969 and 1970 is the most comparable study in recent years. Their study areas were located close to the Kerio River near Lohari which is about 70 km south-west of Balessa Kulal. The area lies in the same ecoclimatic zone as the arid area of Balessa Kulal, Ol Torot and Kargi although the permanent Kerio river clearly ameliorates conditions along its banks.

Grammomys dolichurus and the gerbils *Taterillus nubilus* and *Gerbillus pusillus* were not recorded in either 1979 or 1980 nor was the shrew *Cocidura bicolor*. However, the small numbers of animals caught in the arid areas in the Kulal area make it quite likely that some species have been missed. It is worth noting in this respect that the records of *Grammomys* and *Claviglis* of the R. G. S. expeditions were each based on single specimens recorded in the three years. *Tatera robusta* reported from the Kerio valley was not found around Mt. Kulal but *T. nigricauda* was.

Although *Grammomys* was not caught in the arid sites, it was trapped in the forest on Mt. Kulal and its range might be expected to extend to suitable sites at lower altitudes. Three species of rodents and one unidentified uniformly grey shrew were trapped at an altitude of about 2000 metres on Mt. Kulal. *Myomyscus fumatus* and the shrew were recorded in the grassland and *Claviglis murinus* in the forest. The record of *Myomyscus* from the forest may be due to the proximity of the trap line to grassland. The presence of this species in perennial grassland adjacent to the forest is noteworthy as Kingdon (1975) describes it as primarily a rock-dwelling rat living in rather dry scrubby country on mountain and rock outcrops, while Delany (1975) records it as a species of dry savanna frequently associated with rocky outcrops but also recorded among Borassas palms and acacias. The species was not recorded from the Kerio valley by Coe (1972).

The three specimens of *Grammomys* caught from forest sites are interesting because two of them had ears with a distinct white sub-auricular tuft. The presence of this feature has been used to distinguish *G. cometes* from *G. dolichurus* by Missonne in Meester and Setzer (1977). The skull and head and body for all three specimens were less than the range indicated for *G. cometes*; therefore, the specimens have been provisionally retained as *G. dolichurus*. It appears that the sub-auricular tuft may be a variable feature and in consequence it must be used with caution in identification. Certainly the Mt. Kulal population of *Grammomys* deserves further investigation.

Five specimens of *Claviglis* were trapped in the forest and were all similar in size and appearance, dark grey above and dark grey patchily washed with buff below. This description contrasts markedly with that of two *Claviglis* caught at Ol Torot which were smaller, a light smoky grey above and light grey with buff below, becoming cream on the throat and chin. The average body measurements for specimens from the two sites are given in Appendix 1. An examination of material from intermediate sites as well as more from forest and arid areas could prove interesting.

Studies of the fauna of mountains in equatorial Africa have mainly been of the afro-alpine zone (Coe, 1967), and moist evergreen forests (Rahm, 1966), (Rahm and Christianson, 1963), (Eisentraut, 1963) and Missone (1963).

Delany (1966) trapped mammals on Mt. Moroto in northern Uganda, not far from the Kenya border. Like Kulal, Mt. Moroto is an isolated mountain with montane forest and grass savanna but it differs in being wetter. From trapping sites at about 2800 metres on Mt. Moroto, three species of rodent were recorded: *Praomys morio*, *Lophuromys sikapusi*, differs in the forest and *Otomys irrotatus* and *Lophuromys sikapusi* from the grassland. No shrews were recorded. Thus, from the limited data available, the two mountains, although they have some vegetational similarities, appear to have no small rodent species in common. Both, however, appear to have few species. It is tempting to postulate that the paucity of species on Mt. Kulal is a result of the climatic changes since the last glaciation of East Africa. Recent work on Quarternary environmental changes has been succinctly reviewed by Diamond and Hamilton (1980). The evidence here suggests that glacial periods were dry and interglacials humid. Accordingly, prior to a period of rapid warming 10,000 to 12,000 years ago, montane areas such as the Kenyan highlands were largely under savanna, probably with patches of impoverished montane forest. The area of forest has spread since.

This interpretation of the area's climatic history suggests that the forest on Mt. Kulal was probably established in a period of heavy precipitation in the early post-glacial period of between 7000 and 10,000 years ago. Since then conditions have become drier, thus the period when montane species could have invaded Kulal would have been quite short.

The issue of the isolation of Mt. Kulal is further complicated by the difficulty of dating the changes in the level and extent of Lake Turkana and also the periods of volcanic activity of the Mt. Kulal area since the last glaciation.

Although the relationships between past climate, lake levels, volcanic activity and the history of changes in the topography of the area are by no means clear there appears to be a reasonable likelihood that Mt. Kulal has been ecologically isolated from the surrounding highlands for much of the last 10,000 years.

However, further studies on mammals in grassland and forest sites on Mt. Kulal are required before these ideas leave the realm of speculation. It would be particularly interesting to examine the rodent fauna of neighbouring Mt. Marsabit which is 1800 metres high, i.e. 500 metres lower than Mt. Kulal. If the arid glacial theory holds, then on Mt. Marsabit, being lower than Mt. Kulal, the forest would have had a shorter time to establish itself and hence a shorter period when rodents could have established themselves there before more recent drier conditions isolated the mountain.

Examination of the rodent fauna of the Ndoto mountains, south of Mt. Kulal, might also be profitable as this range is connected with other mountain areas of Kenya and Tanzania by highlands above 1500 metres, i.e. above the present lower limit of the montane zone, and therefore linkup with forest refugia that survived glaciation and from which montane forms could have spread.

6.2 Ecology and general biology

In most instances so few specimens of a species were caught that no reliable conclusions can be drawn regarding the biology of the different species.

Generally the habitats in which the various species were found and their daily activity patterns were in agreement with those recorded by other workers as summarized by Delany (1975), Delany and Happold (1979) and Kingdon (1975).

Where there is good vegetation cover some species such as *Arvicanthis*, *Elephantulus* and *Tatera* occur, whereas species such as *Gerbillus* can survive in more arid sparsely vegetated sites. *Xerus* was observed in a wide range of habitats but not in the driest areas like the sand dune site at Kargi.

The large number of *Acomys* caught amongst the lava outcrops at Kargi parallels the high *Acomys* catch in a very similar site from south of Lake Turkana (Coe, 1972). The only species that appeared strictly diurnal was *Xerus*. Six *Elephantulus* were captured, four during the day and two at night, which agrees with other records of the day and night activity of this species (Kingdon, 1975).

6.3 Trapping success

In both 1979 and 1980 overall trapping success was low. A notable difference between the studies in these two years was that in 1979 snap traps were at least four times as effective as live traps, whereas in 1980 live traps were more than three times as successful as snap traps. The live traps success rates for the two years were similar: 1.9% in 1979 and 1.5% in 1980. It is difficult, therefore, to account for the difference between the snap trap success rates for the two years.

The low trapping success rates in the arid areas near Mt. Kulal were very similar to those reported by Coe (1972) in the Kerio valley, where rates ranged from less than 1.0% to 4.3%. Unfortuantely Coe did not distinguish between live and snap rates so a more detailed comparison cannot be made.

Elsewhere in arid areas of Africa reported trapping rates have been higher. Nel and Rautenbach (1978) working in the Kalahari Gemsbok National Park had rates averaging about 10%.

Trapping rates were also low in the Kulal forest with the success of ground traps varying from 0.2% for live traps to 1.3% for snap traps and an overall trap success of 0.6%. This compares with a rate of 25% from the Mt. Moroto forest where a combination of live and snap traps were used (Delany, 1966).

Our highest live trap rate of any live trap grid in either 1979 or 1980 was achieved in the montane grassland with a success rate of 5.4%. This compares with an 11.4% rate from Mt. Moroto grassland.

6.4 Density estimates

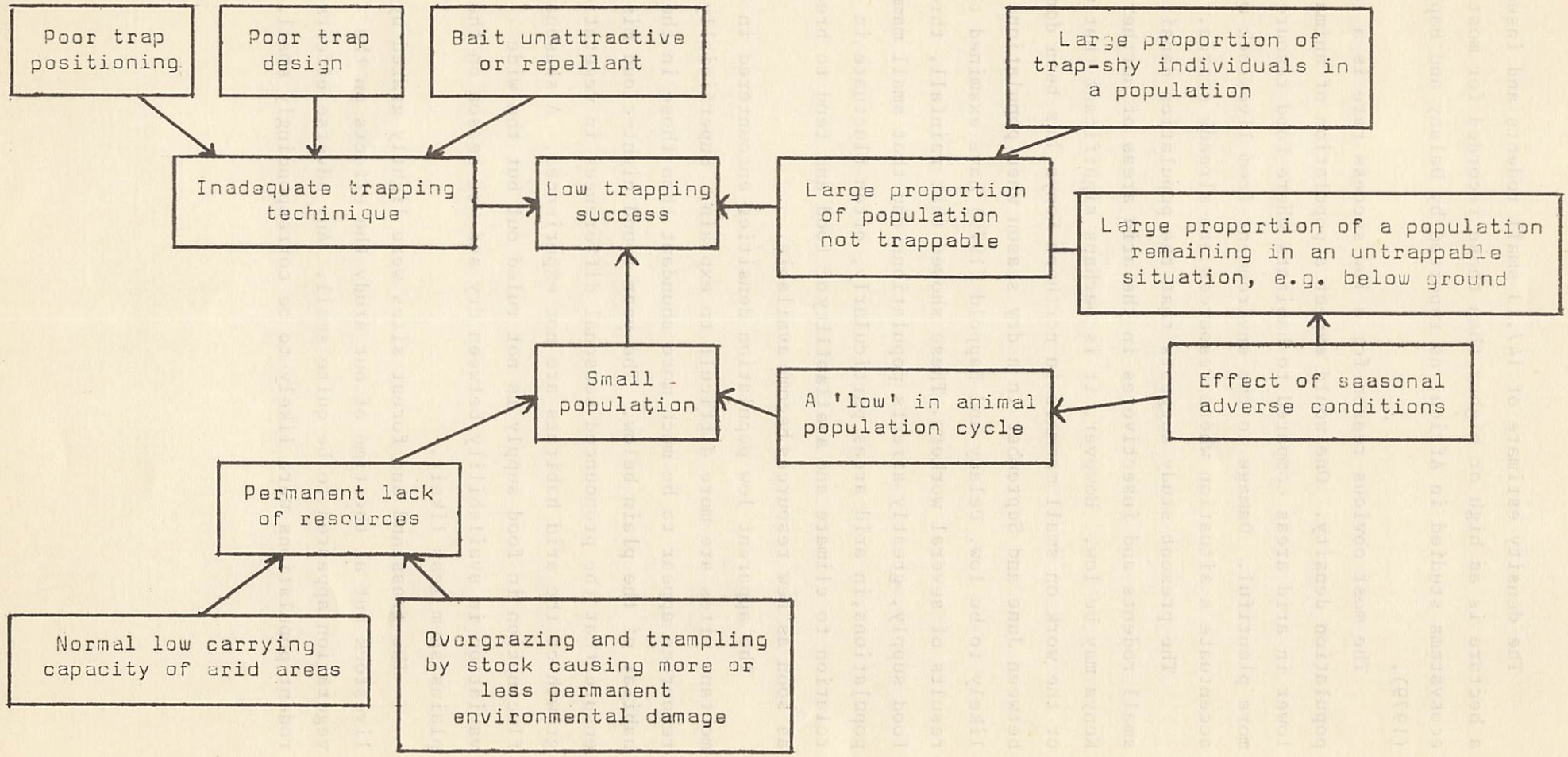
Estimates of densities of small mammals are normally based on the numbers of animals caught. In this study trap success was so low that no accurate estimates of density could be made. It has been assumed that a low trap success is indicative of low population densities and the density 'guestimate' of two or three small mammals a hectare in arid areas was made using this assumption. However, the assumption may only be partially true. Some factors that might contribute towards a low trapping success rate in arid areas are shown in Fig 1.

As far as the current studies are concerned, inadequate trapping technique can be largely ruled out as a major factor. The types of bait and trap employed have been used successfully by many workers and particular care was taken in the positioning of traps. Similar low success rates reported by other workers in the same general area (e.g. Coe, 1972), tend to support this conclusion.

The possibility of a large proportion of the population not being trappable was not investigated. Estimation of the proportion of 'trap-shy' animals in a population is notoriously difficult. It would also be difficult to examine the hypothesis that a large part of the small mammal population spent its time in an untrappable situation, e.g. below ground, at least during the dry season. Certainly some of the species, such as *Tatera*, *Gerbillus* and *Xerus* are known to store food in their burrows, but the extent to which such a practice reduces surface activity and hence trappability is not known.

Coe's (1972) calculations of the population density of small mammals in the south Turkana area imply a large proportion of untrappable animals. Despite low trapping success - virtually the same as in the present work - Coe estimated a density of 147.13 small mammals a hectare (derived by summing Coe's density estimates for *Elephantulus, Arvicanthis, Acomys, Tatera, Taterillus* and *Gerbillus*).

Figure 1. Some Factors leading to a low trap success rate



The density estimate of 147.13 small rodents and insectivores a hectare is as high or higher than those recorded for most ecosystems studied in Africa, as reported by Delany and Happold (1979).

The most obvious reason for a low success rate is a low population density. One would expect a population of animals to be lower in arid areas compared to habitats where food resources are more plentiful. Damage to the environment from livestock would accentuate a situation where resources are already scarce.

The present study suggests that the population densities of small rodents and insectivores in the arid areas of northern Kenya may be low. However, it is perhaps significant that most of the work on small mammals in northern Kenya has been done between June and September in a dry season when populations are likely to be low. Delany and Happold (1979) have examined the results of several workers. These showed that rainfall, through food supply, greatly affects populations and that small mammal populations, in arid areas particularly, often fluctuate in relation to climate and availability of food and tend to breed as soon as new resources become available.

The apparent low population densities encountered in the montane sites are more difficult to explain. Superficially resources appear to be much more abundant than those in the arid habitat of the plain below. The year round night-cloud mists ensure that the pronounced seasonal differences in vegetation growth of the arid habitats are not experienced. A seasonal fluctuation in food supply is not ruled out but the wide variation in availability between dry and wet season on the plains seem less likely.

The grassland and forest sites were lightly grazed by livestock but at the time of our study the effects on the vegetation appeared to be quite small. Any adverse effects on rodent populations were likely to be correspondingly small.

For both arid and montane habitats it is necessary that studies over the entire annual climatic cycle are carried out before the role of rodents in these ecosystems of northern Kenya can be realistically assessed.

7. Acknowledgement

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Appendix 1

Body measurements of *Graphiurus (Claviglis)* sp. caught (a) in forest and (b) arid savanna

Habitat	n	Weight (g)	Head and body (mm)	Tail (mm)	Hind foot (mm)	Ear (mm)
Forest	4	25.1	88.4	79.0	17.6	16.0
		(20.5 - 33)	(82 - 95)	(72 - 89)	(16.5 - 18.0)	(15. - 126)
Arid savanna	1	12	72.5	76.0	14.0	13.8

n = number in sample
figures in brackets indicate the range

SOME ACRIDIDS OF ARID AND SEMI-ARID SOUTHWESTERN MARSABIT DISTICT, NORTHERN KENYA

by
R.O. Okelo

Department of Zoology
Kenyatta University College, Nairobi

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SOME ACRIDIDS OF ARID AND SEMI-ARID SOUTHWESTERN MARSABIT DISTRICT, NORTHERN KENYA

by R. O. Okelo

1. Summary

This work covered 11 months (November 1979 to October 1980) and was carried out within the study area of the UNESCO Integrated Project in Arid Land (UNESCO-IPAL). This area is in western Marsabit District and about 80% of it is semi-arid thorn bush scrubland.

The sites of investigation were two habitats at Gatab (2° 38'N and 36° 56'E; alt. 1800m) on Mt. Kulal; three habitats at Luai (2° 36'N and 36° 57'E; alt. 1350m) and lying about six km south of Gatab; and four habitats at Balessa Kulal (2° 32'N and 37° 04'E; alt. 650m) lying about 60 km southeast of Mt. Kulal within the Hedad Desert (see Map 2). All the three sites have two rainfall peaks in a year, in April and in November. The higher peak is in April. Gatab receives more rain than the other two sites while Balessa Kulal receives the least.

Following identification of species of acridids* associated with the habitats, there were further investigations of numbers of species and their feeding habits. Monthly species densities were investigated in the habitats. Significant differences ($P < 0.05$) were found between the monthly densities of adults and nymphs of the species investigated. Higher densities occurred some time after rains had set in.

* Shorthorned grasshoppers belong to the family *Acrididae* and are referred to in this paper as acridids.

Similar results were obtained for monthly and habitat biomass, but there was significant difference between the habitat biomass of nymphs.

The sex ratios of 17 species were examined and in ten species there were significant differences ($P < 0.05$) between males and females. The sex that occurred in high numbers varied from species to species. In *Gastrimargus verticalis*, for example, males were always more than females.

The numbers of gravid and non-gravid females in species and the numbers of species with nymphs were also investigated monthly for eight months. Over 30% of the species examined each month occurred only as non-gravid adults without nymphs. The percentage of those species with nymphs rose slightly during the dry season. During the same season the percentage of species with gravid females was low.

Using habitat as a resource, niche breadths and subsequently niche overlaps of ten species were calculated by the method of Levin (1968). *Acrotylus longipes*, found in all the four habitats at Balessa Kulal and in the two habitats at Luai, had the highest niche breadth. Niche overlaps were used to estimate the intensity of competition for habitats. Species with higher niche breadths and hence higher niche overlaps avoided competition by colonizing more habitats than their counterparts. Thus *Odontomelus* sp. whose niche - overlap value was 1.07 against 0.55 of *G. verticalis* has avoided competition for habitat with the latter species in this manner.

Relative interaction was calculated from niche overlap data by the method of Price (1971). The results indicated that the main factor determining the intensity of interaction was not the size of the niche breadth but rather the density of a species together with the densities of those it interacted with.

Examination of mandibular structure revealed that the percentage of grass feeders and forb feeders gradually fell with an increase in aridity. It was highest at Gatab and least at Balessa Kulal. This was reversed in the case of the mixed feeders. A lot of work has been done (Chapman, 1964; Gangwere and Ronderos, 1975) to relate mandibular structure to type of plant food material eaten. But little or no work had hitherto been done to relate mandibular structures to aridity of the environment.

Food preference studies were carried out and related to mandibular structures. The results indicated that graminivorous acridids preferred grasses to forbs and vice versa for forbivorous species. Mixed feeders preferred grasses most implying that there is emphasis on grass feeding by mixed feeders in the IPAL study area. Feeding was timed in the laboratory and the results showed that the time taken before a response is made to presented food had some bearing on mandibular structure and type of plant food presented. Thus graminivorous species responded faster to grasses than to forbs.

The amount of oven-dry matter required per gramme live weight of an acridid was calculated. It was shown that smaller acridids required more food per gramme live weight than larger ones.

Acridids were found to consume about 10kg km^{-2} d^{-1} of plant material and this is about 2.17% of primary production. Percentage of primary production consumed varied from time to time in the three sites. On the average it was 2.5% at Balessa Kulal, 3.2% at Luai and 0.8% at Gatab.

Times of active feeding were inferred from changes in crop weight as a percentage of total body weight during the day. The crop percentage method was preferred to the crop weight method. The latter requires that individual acridids be of the same age. In this study individual acridids were caught from the field and therefore were not necessarily of the same age. Feeding patterns were found in general to be similar in most of the Oedipodinae and highest activity occurred around noon. Each sex of *Parasphena kulalenis* (Pyrgomorphinae) had its own feeding pattern that was constant during both dry and wet seasons.

Females fed actively in the morning and noon hours and slowed down in the afternoon. Males fed actively in the morning, less at noon and only slightly in the afternoon.

Some actual feeding was observed in the field and *Dictyophorus griseus*, for example, was observed during such field studies, feeding on leaves of *Aspilia mossambiciensis*.

This study has shown that acridids compete with livestock for food. Field (1979) has shown that camels, sheep and goats combined take 7% of primary production from the IPAL study area, mainly from Balessa Kulal (compare this with 2.5% by acridids).

Since Oedipodinae form the majority, by species, future investigations should go along one of the following lines:

(a) Investigating the role of this subfamily in causing desert encroachment in northern Kenya. This would be worthwhile considering that most of the Oedipodinae such as *Locusta migratoria*, *Oedaleus senegalensis*, *Chortoicetes terminifera* and *Locustana pardalina* are known to cause some damage to vegetation in their respective arid areas of the world.

(b) Carrying out performance studies on one or two species of this subfamily using cultivated crops such as millet, maize and wheat. This would be appropriate considering that some arid-zone agriculture may one day be started in northern Kenya as it is already in the Sahelian zone.

2. Introduction

2.1 Background information

The United Nations conference held in Nairobi in 1977 formally recognized the progressive degradation of the arid and semi-arid regions of the world as a major environmental crisis (Anon., 1977). At the conference the process of desert encroachment was ascribed primarily to the impact of human activity upon soils and vegetation. The United Nations Environment Programme (UNEP) and the United Nations Educational Scientific and Cultural Organization (UNESCO) co-operated on a management-oriented research project to look into causes and effects of desertification and to seek possible remedies for it.

Rather than look at human activity alone, an integrated approach was adopted in which the role of other animals in causing desert encroachment was to be studied.

UNESCO-IPAL activities are centred in semi-arid northern Kenya. The effects of phytophagous insects on vegetation in this area were considered and in the present study acridids were considered as an example and perhaps one of the most important groups of phytophagous insects.

2.2 Study Area

The IPAL study area (see Maps 1 and 2) covers approximately 23,000 km^2. It occupies about 30% of Marsabit District and about 4% of Kenya and lies on the southwestern side of the district.

The climate of the study area has been discussed by Edwards et al. (1979). Due to a wide range of altitudes there is considerable variation in climate. Following the ecological zones of Pratt and Gwynne (1977) the highlands are represented by zone II (humid to dry subhumid). As altitude decreases the zones change to zone IV (semi-arid), zone V (arid) and zone VI (very arid). Most of the IPAL study area is within zones V and VI. This climatic region, the most arid in East Africa, also covers Somalia and Eastern Ethiopia (Griffiths, 1969).

The two main rainfall peaks are April and November. The April peak abates by May and there is usually no rain till the beginning of October. The October rains continue into November and December, and only very little rain occurs during the period before April. Records during the twelve months of study (October 1979 to September 1980) gave total rainfall for Gatab as 494.3 mm, for Luai 241.0 mm and for Balessa Kulal 128.8 mm.

At Gatab, on Mt. Kulal, mist or low cloud occurs. It has been observed that trees, mainly *Juniperus procera*, provide a large area upon which the moisture in the cloud may condense and fall to the ground.

Associated with this is a distinct patch of understorey which is larger on the leeward side than on the windward side of each tree. The understorey appears to be dependent on this occult precipitation for its survival (Edwards et al., 1979).

The annual range of mean monthly temperature is small, reaching 4.0°C at Balessa Kulal and only 2.6°C at Gatab. January and February are relatively warm months when dry northeasterlies flow across northern Kenya. Clear skies allow high levels of insolation and mean daily maxima of 35°C are recorded at Balessa Kulal (600 m elevation) and 23.5°C at Gatab (1800 m elevation). Very low minima are recorded during this time at Balessa Kulal (15.4°C) and at Gatab (16.2°C). There was, however, no weather station at Luai, except for a storage rain gauge.

The geology, topography and drainage systems of the area have been extensively discussed by the author of an FAO working paper (Anon., 1971) and Herlocker (1979). Two major geological formations occur within the IPAL study area: Tertiary Pliocene recent volcanic lavas around Kulal and Marsabit Mountains, and around the Huri Hills; and Quarternary Pleistocene sediments derived from Precambrian gneisses of the mountains to the south and southwest (Map 2). These sediments also cover the area of Lake Turkana and the deserts of Chalbi, Koroli, Hedad and Kaisut. Two minor geological formations also occur. The Middle to Late Pleistocene sandstones and shales lie southeast of Maikona (Map 2) between the lava and the Chalbi Desert. The Precambrian gneisses lie to the southwest edge of the study area. Though small this formation is important as it is the source of the Quarternary sediments.

The study area is an extensive plain at an elevation of 530-760 m the largest of which make up the Koroli, Hedad (Balessa Kulal lies here) and Kaisut areas. It rises gently southwestwards from the edges of Marsabit lava to the base of mountains in south and southwest (Map 2). The Asie Hills, a low outlier of Mt. Kulal, extend for about 50 km northeast of it to the edge of the Chalbi Desert.

Seventy seven per cent of the study area is within the drainage system leading to the Chalbi Desert. This drainage system acts as a sump for an interior drainage system. Other drainage systems lead into Lake Turkana from the western slopes of Mt. Kulal and Mt. Nyiru; and into Milgis River from the southwestern slopes of Marsabit Mountain and from the Kaisut area. The Milgis River then flows into swamps southeast of Marsabit Mountain. Subterranean drainage has been reported bearing water in the lava formation north of Marsabit Mountain (Anon., 1971).

The vegetation map of Marsabit District prepared by FAO (Anon., 1971) was the first approximation to a detailed classification and delineation of plant communities in the district. Aerial photographs were used to map the vegetation. In a more detailed study Herlocker (1979) produced a vegetation map for the western part of the district. This was based on features observed during extensive journeys made in the study area. In this map, the vegetation classification of Pratt and Gwynne (1977) has been followed. Unlike the FAO map where emphasis was placed on vegetation units as determined by geomorphological features, here the criteria are primarily physiognomic (e.g. forest, woodland) modified by functional criteria (e.g. evergreen, deciduous), physiographic criteria (e.g. upland, lowland) and compositional criteria (e.g. *Combretum*, *Acacia*).

The people, together with their large herds of livestock, have some real impact on the vegetation of this area. The animals eat and trample vegetation while people cut a lot, mainly thorny plants, for fencing. The main tribes in this area are the Rendille and the Gabbra. Both are nomadic pastoralists keeping camels, sheep and goats and they do not overlap geographically because of antagonism in the past (Lamprey, 1978). Small numbers of cattle-keeping Boran and Samburu occupy the more mountainous fringes of the area. The human population is very low, lower than one person per km^2, and the centres of livestock and human concentration occur near springs, wells and bore holes.

During and immediately following rain there is a traditional dispersal of nomadic family groups into areas where rain has fallen to take advantage of the new growth and the rain pools. Women and children and older people remain near villages and keep with them some animals they need for milking. The young men take away the bulk of the livestock to the surrounding country.

Very little has been documented regarding the amount of plant food eaten by wild animals; including phytophagous insects, in this area. Although usually solitary, certain acridid species are known to become gregarious and form swarms which migrate and cause heavy losses to vegetation. Acridid species that behave in this way are known as locusts. It is important to note, however, that many acridid species have the potential to become gregarious and migrate in swarms. For example, in recent years *Oedaleus senegalensis* has attained that status in the Sahel and caused damage to millet and much work, such as that of Boys (1978), is already directed to this species.

3. Objectives of the study

Acridids are phytophagous and may directly compete with mammals for the available grass and forbs and this contributes to desertification. It is for this reason that this study was initiated. Primarily it was intended to determine:

(a) The species of acridids and plants in the study sites and change, with time, of density and biomass of nymphs and adult acridids and plant species fed on.

(b) The amount of plant food material consumed and the percentage of primary production removed.

(c) Times of the day when feeding activity occurs.

(d) The relationship of mandibular adaptation to feeding and to aridity factors of the study sites.

(e) The effect of rainfall on the change in percentage composition of developmental stages of acridids in semi-arid environments and population changes of nymphs and adults with time.

(f) Sex ratios of various species and also the composition for habitat by various species.

4. Materials and methods

4.1 Study sites

The three study sites, Gatab(2° 38'N and 36° 56'E; elevation 1800 m), Luai(2° 36'N and 36° 57'E; elevation 1350 m) and Balessa Kulal(2° 32'N and 37° 04'E; elevation 650 m) were selected for ease of transport and differences in altitude, vegetation and climate. Each site was divided into various habitats.

Gatab lies within an area of evergreen bushland and in Zone 3 of Herlocker (1979). The two habitats selected for study were Upper Gatab and Lower Gatab. The former borders the montane forest and has a more dense bush of Zone 3 than the latter.

Luai lies 5 km south of Gatab and is within deciduous *Acacia* woodland with a *Duosperma eremophilum* understorey. Three habitats were selected for study, two in Zone 9 and one in Zone 10 (Herlocker, 1979). The two in Zone 9 were distinguishable by one being an enclosure and the other open grazed ground.

Balessa Kulal is about 60 km from Gatab, but only 20 km as the crow flies southeast of Gatab. It lies at the junction of the lava and sand sediments of Hedad. Four habitats were selected for study:

lava lying in Zone 67,
enclosure within Zone 13,
sand river bed also in Zone 13, and
Acacia reficiens habitat in Zone 31.

4.2 Rainfall record at the study sites

Daily standard and storage types of rain gauges were located in various places within the IPAL study area. The former was located at Gatab and at Balessa Kulal. Daily rainfall records from these two stations were entered in a Metform 1123. Normal and occult precipitations were compared from weekly rainfall records kept for two daily standard rain gauges sited at Gatab, one in the open on the windward side of a *Juniperus procera* tree and the other on the leeward side of the same tree. The storage rain gauge at Luai was read once a month as were the other twelve such storage rain gauges in other places within the study area. Into every storage rain gauge a thin layer of vehicle sump oil was added to minimize evaporation. Monthly rainfall records were kept from October 1979 to September 1980.

4.3 Population studies

4.3.1 Acridid species composition

At least twice a week during the course of this study, acridids were collected within the Gatab habitats, and at least twice monthly within the habitats at Luai and at Balessa Kulal. Acridids were caught using a sweep net and killed in a jar using chloroform which was preferred to cyanide because of the scarcity of water which might have been needed to wash off any cyanide traces in case of contamination.

The killed specimens were labelled and pinned into insect boxes with insect pins. The boxes were cartons with styrofoam sheets at the bottom. The boxes proved ideal for light aircraft transport to Nairobi for indentification when necessary. Either naphthalene balls or p-dichlorobenzene crystals, whichever was available, were used to preserve the specimens.

The specimens were identified using keys provided by Kevan (1946); Dirsch (1951, 1954, 1965, 1968); Jago (1963, 1967, 1971); Hollis (1966, 1967, 1968); and Uvarov (1966). Those that could not be identified and confirmed were sent to Dr Nicholas David Jago of the Centre for Overseas Pest Research, for identification and confirmation.

The specimens were then assigned to the study sites and composition by subfamilies calculated for the three study sites combined and also for each individual site.

4.3.2 Acridid density

Acridid density was investigated monthly for each of the nine study habitats for ten months at Gatab and Luai, and for nine months at Balessa Kulal. Balessa Kulal was not sampled in October 1980 because of an 'invasion' of the site by lions.

Various acridid species were identified in flight by colour of hind wing, size, type of flight (e.g. jerky, slow, fast), type of jump (e.g. long, short) and sound produced.

Twenty line transects, 10 m by 2 m, were taken at each habitat on a bright sunny day when acridids were active. Gatab habitats were sampled thrice a month while those at Luai and Balessa Kulal were sampled twice a month. An observer walked along the transect very slowly, cautiously disturbing vegetation (where this was present) with a sweep net. The species and number of individuals, adults and nymphs, that were disturbed were recorded. No attempt was made to treat the sexes separately as this would not be possible by this method. Scheepers and Gunn (1958) used a more or less similar 'flushing method' to estimate the population of *Nomadacris septemfasciata* in its outbreak area in East and Central Africa.

Acridid density was calculated per square metre for nymphs and adults for each site, for each habitat and during each month of sampling. The data were related to amount of rainfall, and consequently vegetation, in order to assess the impact of rainfall and vegetation on the population acridids.

Double classification analysis of variance (Parker, 1979) was carried out to investigate whether differences in densities of nymphs and adults between habitats and between months in relation to rainfall were significant.

4.3.3 Acridid biomass

Nymphs and adults of both sexes were caught in the field using a sweep net. These were kept in a dry 400 ml Kilner jar with a perforated metal lid. Adults and nymphs were maintained in separate jars and in each case a record of self-mutilation of hind femora was kept together with the right individual acridid and later weighed together. Live weights were taken at the field laboratory at Gatab on Mt. Kulal within 1 to 5 hours after capture, with the aid of a Shirai beam balance. The individual live acridids were weighed, each in a preweighed corked specimen tube. Oven-dry weights were also taken using an IPAL generator-powered oven at 100°C. Weighing of live acridids was not done immediately in the field because of strong winds that disrupted the balance.

The mean live and mean oven-dry weight of females, males and nymphs of species caught were calculated from the data collected during the study. The study sites were compared using mean live and mean oven-dry weights of the species that were caught.

For comparison with large herbivores (camels, sheep and goats), live weights were used instead of oven-dry weights.

Mean live weights of adults and nymphs of a species were calculated and multiplied by corresponding density to obtain the biomass of adults and numphs, respectively. The biomass of adults and numphs expressed as g m^{-2} was calculated for each habitat and for each study site three times a month for Gatab and twice a month for Luai and Balessa Kulal and related to the amount of rainfall and consequently vegetation for the month.

The significance of differences observed in the biomass during the months of study in the habitats was tested using double classification analysis of variance (Parker, 1979).

4.3.4 Sex ratio

The individuals of various common species at the time of sampling were caught at random for two hours. The captured individuals were counted to give the proportions of either sex. This was repeated twenty times for each species. Significant departures from the expectation in the case of each species were tested using Chi-square (Parker, 1979).

4.3.5 Developmental stages

In order to investigate the dynamics of developmental stages of the acridid community, females of species were examined each month for eight months and records kept of the number of species examined, the percentage of species that occurred as adults only, the percentage of species with nymphs and the percentage of species with both nymphs and gravid females.

Percentages were related to the average amounts of rainfall for the three sites during each month. At least twenty females of each species were examined before concluding that a species had no gravid females during that month.

Each of the sites was investigated for the dynamics of developmental stages and results related to monthly rainfall amounts.

4.3.6 Niche overlap

Niche overlap was used to estimate the intensity of competition between species for habitats.

Mean densities, for nine months, of adults of ten species in which this was investigated were calculated for each of the nine habitats. The results were used to calculate the niche breadth of each species by the method of Levin (1968). The niche breadth of each species was used to calculate the corresponding niche overlap of a species over the other (Levin, 1968).

For each species, values of niche overlap were obtained that corresponded to the number of counterpart species it could interact with. The mean of these values for a species represented an estimate of the relative interaction between contiguous species (Price, 1971).

4.4 Feeding behaviour

4.4.1 Mandibular structure

The mandibles of acridid species drawn from all the sites were dissected out with the scalpel blade and examined under a dissecting microscope for classification by feeding habits using the method of Chapman(1964) and Gangwere and Ronderos (1975). The resulting categories were related to estimated mean annual precipitation and consequently vegetation of each of the three study sites (Herlocker, 1979).

4.4.2 Laboratory observation on feeding habits

Acridids were caught from the field and each individual placed in an 870 ml Kilner jar and left for 24 hours to acclimatize. The Kilner jars had tops of perforated paper held tight with rubber bands. Any records of self-mutilation of hind femora were kept and treated as previously described.

At the end of 24 hours the weights of the acridids were taken using a Shirai beam balance, previously described, and recorded. Each acridid was given a known weight of plant food material using a 'no-choice test' described by Adams and Bernays (1978). The cut ends of plant food material were put in tissue paper soaked in tap water. The moist tissue paper was to reduce water loss through the cut end. A control plant food material of the same species as that supplied was treated in a similar manner and placed in a jar of the same capacity, but without an acridid. Care was taken to use similar plant parts that were in more or less the same condition.

The experimental set up was left at room temperature for 24 hours on a wooden bench fitted to a wooden wall in the field laboratory at Gatab.

At the end of 24 hours, the acridids, and test and control plant food material, were removed from the jars and weighed separately and the weights recorded. The percentage loss in weight of the control was calculated and used to calculate the amount of food eaten. Fresh weight of food consumed was calculated by adding the product of the percentage loss in weight of the control and the original weight of food supplied to the weight of food left over, and then subtracting the result from the original weight of food supplied.

Similar fresh plant material of the species supplied was weighed and then oven dried at 100°C using the IPAL generator-powered oven to determine the dry-matter weight. The percentage dry matter was used to determine the dry matter eaten.

In all cases sexes were treated separately and each sex was treated either as unstarved or starved depending on whether the preceding meal had been eaten or not. Failure to eat the food presented was taken to be an indication of non-preference. Late instar nymphs were also used in the trials.

Forty three plant species were tried, eleven grasses and thirty two non-grasses, on twenty three acridid species. Of these acridid species, seven, five and eleven were graminivorous, forbivorous and mixed feeders respectively. Percentage successes of various mandibular feeding adaptations with grasses and non-grasses were calculated.

Approximate rate of response to presented food was also calculated. The insect was observed constantly for the first twenty minutes in order to note the shortest time length, if any, taken before approaching, probing, biting and eating the food presented. The observations were carried out, two to five times a week, for 9 hours during day time for eight months.

Individuals of graminivorous species were observed as controls presented with non-grasses and those of forbivorous species presented with grasses. Mixed feeders were presented with grasses and non-grasses separately. Starved and unstarved individuals of either sex and late instar nymphs were treated separately.

A total of 964 approximations were made, 691 on females, 212 on males and 61 on numphs. There were 360, 107 and 25 approximations on unstarved females, males and nymphs respectively; and 331, 105 and 36 on starved individuals in that order.

The degree of preference of 31 plant species by acridids was estimated by expressing the number of times a species of plant was eaten as a percentage of the total number of times it was presented to the various acridid species. Food preference was scored on an arbitrary scale ranging from 0-20%(least preferred) to 81-100% (most preferred).

Oven-dry weights of plant food material consumed were expressed as g/g live weights of the acridids tested. For each of the three study sites data were collected for nymphs and for adults during the two wet seasons (November and December 1979, and April and May 1980) and two dry seasons (January and March 1980; and June, July and August 1980). The mean g/g live weights of nymphs and adults were than calculated.

Food ingested by acridids was calculated by multiplying g/g live weights of acridids used in the feeding trials by estimated biomass, to give an estimate of dry matter of plant food removed from a square metre per day.

4.4.3 Field observation on feeding habits

During the study period a record was kept of the species and parts of the plant on which acridids fed in selected habitats in the field. Observations were made using a pair of Greencat binoculars (x320) from a distance of approximately six metres.

4.4.4 Times of active feeding

Three feeding time periods of 0800-1000 h, 1100-1300h, and 1400-1600h were selected for observation considering weather conditions. Individual adult acridids were captured, using a sweep net, during the last hour of the feeding time period and killed as previously described. Each killed individual was weighed intact within 1 to 5 hours as previously described. The crop was removed and the individual reweighed. The difference in weight gave the weight of the crop which was then expressed as a percentage of total body weight.

Data collected during seven months (December 1979, April and May 1980 as wet periods; and January, March, June and July 1980 as dry periods) were separately considered under dry and wet periods, feeding time periods and sexes. In all there were 1338 individuals weighed from 12 species, and at least 20 individuals of a sex were weighed for each feeding time period. Mean percentage of crop weight over intact body weight for each sex of a species during feeding time periods were then compared and feeding activity inferred.

During the months of April and May 1980 three species, *Parasphena kulalensis*, *Aiolopus thalassinus* and *Acrotylus patruelis*, were investigated in a similar manner at hourly intervals from 0700h to 1600h. The crop weight as a percentage of total body weight of the species caught was considered an indication of the amount of food taken during the preceding hours. The three species were investigated in detail because they occurred in large numbers at Lower Gatab habitat during these two months.

5. Results and discussion

5.1 Rainfall at Gatab, Luai and Balessa Kulal study sites

Monthly rainfall records (mm) for twelve months, October 1979 to September 1980, and the actual and occult precipitation were as indicated in Figures 1 and 2 respectively.

Fig. 1

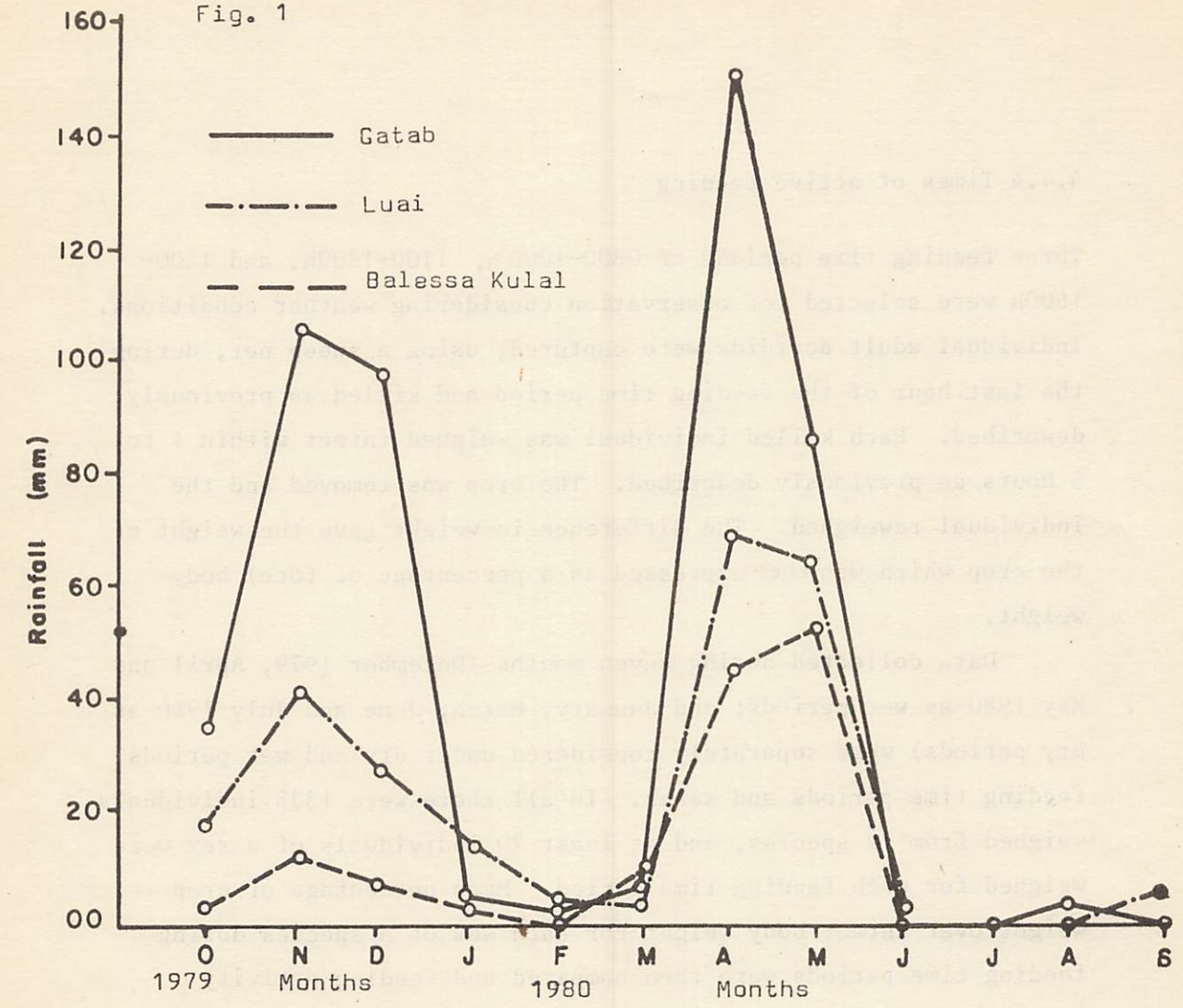
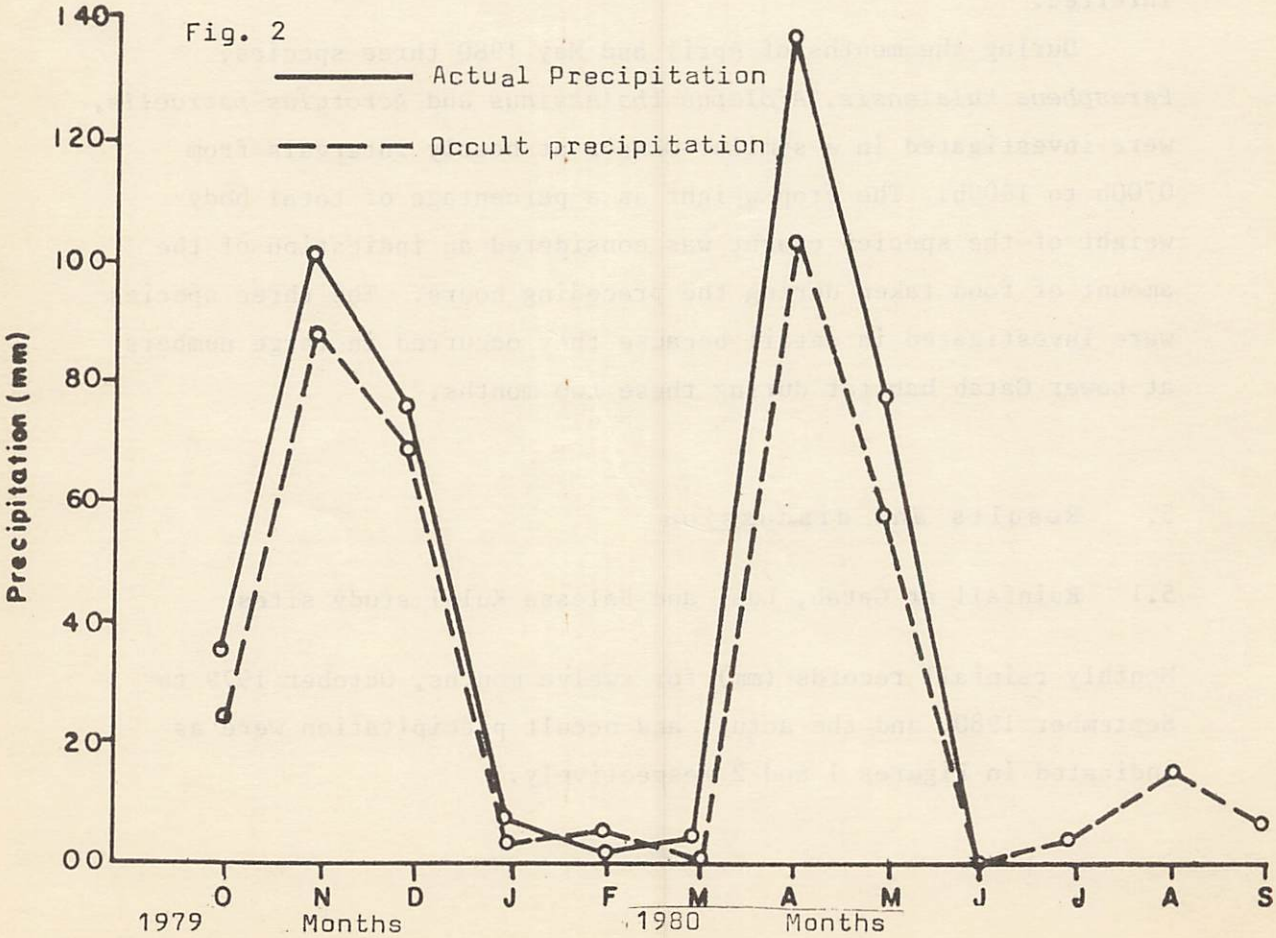

Gatab
Luai
Balessa Kulal
Rainfall (mm)
160
140
120
100
80
60
40
20
00
O N D J F M A M J J A S
1979 Months
1980 Months

Fig. 2


Actual Precipitation
Occult precipitation
Precipitation (mm)
140
120
100
80
60
40
20
00
O N D J F M A M J J A S
1979 Months
1980 Months

Both Gatab and Luai had two rainfall peaks, in April and November, with the higher peak in April. At Balessa Kulal the two peaks occurred in May and November, with the higher peak in May. The sites with higher elevations received more rainfall on the average. During the drier months actual precipitation was lower than occult precipitation.

5.1.1 Discussion

Although Gatab (1800 m) received more rain, particularly during the peak months of April and November, than the other two study sites, Luai (1350 m) received more rain in January and February 1980. It is possible that the strong winds that occurred with rain during these months deflected some rain as it fell towards Luai instead of all of it falling at Gatab.

The quantity and quality of vegetation depends on the amount of rainfall that falls at a place during a particular length of time. Green and fresh vegetation occurred at these study sites during the months of higher rainfall. During dry months only those deeply rooted plants were green, but annuals, with shallow roots, were only available as 'standing dead'.

Mist is known to contribute 40-94% of total precipitation on high ground in South and South-West Africa (Marloth 1904, 1907; Nagel 1962). Trees, mainly *J. procera*, on Mt. Kulal provide a surface upon which moisture in the cloud may condense (Edwards et al., 1979) and fall to the ground. This moisture supports distinct patches of understorey, larger on the leeward sides of such trees than on the windward sides. *Myrsine indica* dominated such understorey (Edwards et al., 1979). However, during this study it was noted that during rains *Crinum kirkii* and *Bulbine abyssinica* occurred within or in the vicinity of such understorey.

A feature revealed by Figure 2 is that whereas there may be no rainfall, the occult precipitation may still occur provided there is cloud, moisture and a surface upon which such moisture may condense and fall.

Such was the case in July, August and September 1980. There was virtually no actual precipitation during these months.

5.2 Acridid population studies

5.2.1 Acridid species composition

Acridid species composition by subfamilies for all sites combined and separately in each study site (Table 2) indicates that the subfamily Oedipodinae had the largest number of species with nearly half of them at Luai. The next subfamily, with eleven species, and with a majority at Balessa Kulal, was Gomphocerinae. Eyprepocnemidinae came next with six species with over half of them at Luai. Thericleinae and Romaleinae had the least number of species with the former subfamily having only one species which occurred only at Gatab and the latter subfamily also having only one species which occurred only at Luai.

Some species occurred in more than one study site. *Acrotylus longipes* and *Pnorisa squalus* occurred at Luai and at Balessa Kulal; and at Gatab and at Luai respectively. It is for this reason that the overall total of sites taken individually would be 74 instead of 57 (Table 2).

The species encountered are listed in Table 1 under their respective families and subfamilies.

Table 1

Acridid species by families and subfamilies

		Study site
EUMASTACIDAE - Thericleinae		
Brachytyphus rotundifrons	Burr	Gatab
ACRIDIDAE - Pyrgomorphinae		
Chrotogonus homalodemus	Blanchard	Balessa Kulal
Phyteumas purpurascens	Karsch	Gatab

(Table 1 contd.)

Dictyphorus griseus Reiche and Fairmaire	Gatab
Parasphena kulalensis Kevan	Gatab and Luai
Parasphenula sp.	Gatab
Pyrgomorpha conica Karsch	Balessa Kulal
ACRIDIDAE - Romaleinae	
Acrostegastes glaber Karsch	Luai
ACRIDIDAE - Caliptaminae	
Acorypha glaucopsis Walker	Luai
Acorypha pulla Uvarov	Luai
Acorypha ornatipes Uvarov	Luai
Sphodromerus calliptamoides Uvarov	Gatab
ACRIDIDAE - Eyprepocnemidinae	
Eyprepocnemis plorans Charpentier	Luai
Heteracris annulosa Walker	Balessa Kulal
H. coerulescens Stal	Gatab, Luai and Balessa Kulal
H. rantae Uvarov	Balessa Kulal
Taramasus cunctator Karsch	Gatab and Luai
Cataloipus fuscocoeruleipes Sjostedt	Gatab and Luai
ACRIDIDAE - Catantopinae	
Ischnansis gracilis Schulthes	Balessa Kulal
Phaeocatantops decoratus Gerstaecker	Gatab
Catantops axillaris Thunberg	Gatab, Luai and Balessa Kulal
ACRIDIDAE - Cyrtacanthacridinae	
Anacridium melanorhodon Walker	Luai and Balessa Kulal
Cyrtacanthacris tatarica Linn.	Gatab, Luai and Balessa Kulal
Acanthacris ruficornis Fabricius	Gatab
ACRIDIDAE - Acridinae	
Odontomelus sp.	Gatab and Luai
Duronia chloronota Stal	Luai and Ol Turot near Balessa Kulal
Gymnobothrus inflexus Uvarov	Gatab
Gymnobothrus linea-alba I. Bolivar	Gatab
ACRIDIDAE - Oedipodinae	
Aiolopus thalassinus Fieber	Gatab
Sphingonotus canariensis Sauss.	Luai
S. rubescens Walker	Balessa Kulal
S. savignyi Sauss	Balessa Kulal
S. turkanae Uvarov	Luai and Balessa Kulal

(Table 1 contd.)

Pycnodictya galinieri R. & F.	Luai
Chlaobora dimorpha Uvarov	Luai
Scintharista notabilis Walker	Balessa Kulal
Gastrimargus Verticalis Ṣauss.	Gatab
Oedaleus instillatus Burr	Luai
O. senegalensis Kraus	Balessa Kulal
Morphacris fasciata Thunberg	Gatab
Acrotylus longipes Charpentier	Balessa Kulal
A. ndoloi Kevan	Luai
A. patruelis Herrich-Schaeffer	Gatab
ACRIDIDAE - Truxalinae	
Truxalis burtti Dirsh	Balessa Kulal
T. conspurcata Klug	Luai
T. grandis Klug	Gatab
ACRIDIDAE - Gomphocerinae	
Sporobolus jacksoni Kevan	Balessa Kulal
Ochrilidia gracilis Krauss	Balessa Kulal
O. harterti salfiana Uvarov	Balessa Kulal
Platyternodes rudolfi Uvarov	Balessa Kulal
Stenohippus sp.	Luai
Leva aethiopica I. Bolivar	Balessa Kulal
Pnorisa squalus Stal	Gatab and Luai
Dnopherula werneriana Karny	Luai and Balessa Kulal
Rhaphotittha levis Karsch	Luai
R. nyuki Sjostedt	Balessa Kulal
Afrohippus brevipennis Miller	Luai

Table 2

Acridid species composition by subfamilies
in Gatab, Luai, and Balessa Kulal study sites

Subfamily	Number of species per site			Total
	Gatab	Luai	Balessa Kulal	number of species
Thericleinae	1	0	0	1
Pyrgomorphinae	4	2	2	6
Romalienae	0	1	0	1
Calliptaminae	1	3	0	4
Eyprepocnemidinae	3	4	3	6
Catantopinae	2	1	2	3
Cyrtacanthacridinae	2	2	2	3
Acridinae	2	2	1	4
Oedipodinae	4	8	6	15
Truxalinae	1	1	1	3
Gomphocerinae	1	5	7	11
Total	21	29	24	57

5.2.2 Discussion

The results show that the species of the subfamily Oedipodinae are the most dominant in all sites investigated. More or less similar results were obtained by Okelo and Simatura (1980). All species of Oedipodinae, except *Tropidolophus formosus*, are geophilous (Otte, 1970) and have a preference for bare ground. The IPAL study area is semi-arid with large portions of scattered bare ground.

The Gomphocerinae had a higher number of species next to Oedipodinae. The abundance of the Oedipodinae and the diversity of species of the Gomphocerinae are probably explained by the fact that the study area is actually a relatively recently dessicated savannah (Uvarov, 1938b).

That Balessa Kulal, a more arid site, should have more species than Gatab, a less arid site, is worth noting. Most of the species at Balessa Kulal are widely distributed in Africa south of the Sahara (Dirsh, 1965) and this suggests further that the IPAL study area is a recently dessicated savannah. According to Uvarov (1938b) this part of Kenya received its desert fauna from Somalia in the east and not from the Sahara in the north. Such desert fauna might not have penetrated into high areas such as Mt. Kulal on which Gatab lies. The reason for Balessa Kulal having more species may be that it has two sources of acridid fauna: desert fauna from Somalia and typical savannah fauna from this recently dessicated savannah region. However one species of the subfamily Pyrgomophinae, *P. kulalensis*, did not occur at Balessa Kulal at all. That this species was not encountered at such lower altitude conforms with the findings of Kevan (1946).

The level of the species diversity at Luai indicates that this site, apart from receiving some desert fauna, still has not been dessicated to an extent that would eliminate most of the savannah fauna. As a result, the site has the highest species diversity of all the three study sites.

5.2.3 Acridid density

Total densities were higher in the wetter Gatab throughout the period of this study except in December 1979 and June 1980 when Luai had the highest density (Table 3). The data also show that the density of nymphs was often lower in many species than that of adults. The densities of nymphs and adults for each habitat each month are indicated in Table 4 and no significant difference was observed in the densities of nymphs between the habitats ($P > 0.05$), but there were some significant differences between the months ($P < 0.05$) (Table 5).

The differences between habitats and months with respect to adult densities were significant ($P > 0.05$). After the long rains in April the total population at Gatab reached a peak in May while at Luai and Balessa Kulal the peaks were reached in June and July respectively. In some species, such as *Odontomelus* sp., nymphs were more numerous than adults at certain times of the year.

Table 3

The total density m^{-2} of nymphs and adults for each study site each month (November 1979 to October 1980 inclusive)

Month	Density m^{-2} at the study sites					
	Gatab		Luai		Balessa Kulal	
	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults
November	0.010	0.385	0.027	0.168	0.001	0.031
December	0.005	0.094	0.023	0.131	0.009	0.028
January	0.032	0.091	0.018	0.078	0.011	0.026
March	0.018	0.118	0.005	0.039	0.006	0.014
April	0.005	0.185	0.006	0.061	0.002	0.020
May	0.015	0.388	0.108	0.039	0.018	0.021
June	0.078	0.150	0.011	0.263	0.005	0.086
July	0.259	0.277	0.016	0.308	0.022	0.303
August	0.021	0.325	0.001	0.150	0.005	0.104
September	0.001	0.414	0.003	0.096	0.004	0.070
October	0.009	0.274	0.003	0.007	-	-

Table 4

The density m^{-2} of nymphs and adults for each habitat each month

Months and developmental stages		Habitats								
		1*	2	3	4	5	6	7	8	9
Nov	Nymphs	0.025	0.013	0.018	0.016	0.046	0	0.005	0	0
	Adults	0.319	0.456	0.287	0.094	0.014	0.064	0.034	0	0.010
Dec	Nymphs	0.007	0.003	0.016	0.028	0.026	0	0.013	0.005	0
	Adults	0.084	0.103	0.143	0.176	0.073	0.023	0.028	0.050	0.010
Jan	Nymphs	0.038	0.025	0.013	0.012	0.029	0	0.008	0	0.005
	Adults	0.072	0.109	0.076	0.085	0.074	0.015	0.018	0.040	0.031
Mar	Nymphs	0.024	0.012	0.003	0.009	0.003	0	0.008	0.003	0
	Adults	0.092	0.143	0.045	0.047	0.026	0.008	0.009	0.021	0.019
April	Nymphs	0.006	0.003	0.008	0.006	0.005	0	0	0	0.008
	Adults	0.196	0.175	0.053	0.051	0.080	0.014	0.027	0.018	0.019
May	Nymphs	0.016	0.013	0.008	0.148	0.169	0.036	0.003	0.008	0.023
	Adults	0.247	0.528	0.050	0.034	0.034	0.028	0.028	0.011	0.015
June	Nymphs	0.085	0.071	0.026	0.005	0.003	0	0.005	0.013	0
	Adults	0.156	0.144	0.162	0.353	0.275	0.129	0.071	0.087	0.058
July	Nymphs	0.226	0.291	0.016	0	0	0.011	0.035	0.020	0
	Adults	0.334	0.219	0.203	0.045	0.306	0.394	0.347	0.281	0.189
Aug	Nymphs	0.033	0.008	0	0	0.003	0	0.005	0.008	0.005
	Adults	0.307	0.343	0.181	0.176	0.094	0.130	0.133	0.098	0.053
Sept	Nymphs	0.006	0.013	0	0	0.003	0	0.005	0.005	0.002
	Adults	0.279	0.547	0.083	0.141	0.063	0.031	0.093	0.109	0.047

* Key

1 - Upper Gatab habitat

2 - Lower Gatab habitat

3 - Luai enclosure habitat

4 - Luai grazed habitat

5 - Luai *A. etbaica* habitat

6 - Balessa Kulal lava habitat

7 - Balessa Kulal enclosure habitat

8 - Balessa Kulal sand river bed habitat

9 - Balessa Kulal *A. reficiens* habitat

Table 5

Double-classification analysis of variance
for density of nymphs and adults during ten months

(a) Nymphs

Source of variation	SS	df	MSS	F
Between habitats	0.0231	8	0.0029	1.71
Between months	0.0350	9	0.0039	2.29*
Error	0.1219	72	0.0017	
Total	0.1800	89		

(b) Adults

Source of variation	SS	df	MSS	F
Between habitats	0.4420	8	0.055	7.75*
Between months	0.4610	9	0.0039	2.29*
Error	0.5140	72	0.0017	
Total	1.4170	89		

* Significant difference ($P < 0.05$)

5.2.4 Discussion

The high densities observed in Gatab and Luai (Table 3) correspond with the rains of November and April which rendered conditions favourable for breeding. Attempts to develop semi-arid lands using irrigation would make such environments favourable for acridid population increase and hence crops grown in such situations would be liable to infestation by acridids. This has been reported in the case of *D. moroccanus* in the Syrian desert (Uvarov, 1957).

More thought would therefore be essential before initiating any form of agricultural development in arid and semi-arid lands, particularly regarding the kind of crops to be cultivated.

The peak populations at Gatab (in May), Luai (in June) and Balessa Kulal (in July) (Table 3) are an indication that the areas at lower altitudes have an increase in population somewhat later after the long rains. The occult precipitation and dew from mist at Gatab during dry seasons support the growth of certain vegetation which subsequently supports the development of hoppers of certain species so that by the time the April rains set in there is already a higher level of population at this site than at Luai and Balessa Kulal. Further, the favourable conditions at Gatab support the continuous breeding of certain species, such as *P. decoratus*, a feature not found at the sites with lower elevation. At lower sites green growth is dependent on rains. The acridids depend on the new growth for oocyte development and this may explain the much later rise in total population after the rains at the lower sites.

A much higher total density of acridids at Luai than of acridids at Gatab and Balessa Kulal in December 1979 (Table 3) was due to the appearance of adults of *O. instillatus* at this site. This species was recorded here in November. By late December 1979 its nymphs appeared but there was virtually no nymphal or adult individual of this species towards the end of January 1980 and it was never seen again during the study period. The species must have been on its migratory movements. Kevan and Knipper (1955) observed this species flying in swarms at night in northeast Kenya.

Some acridid species attained very high densities and such densities undoubtedly cause damage to vegetation (Le Pelley, 1952; Boys, 1978). It is therefore maintained in this paper that acridid study should be taken seriously. No species should be regarded as of little importance and therefore receive little attention. Time, money, and manpower will obviously be required. It may be argued that there is no real and immediate necessity to warrant such an undertaking.

But at the same time, money and manpower will still be required should an unexpected outbreak of some acridid species occur.

That there was significant variation in the density of nymphs between the months ($P < 0.05$) and not between habitats ($p > 0.05$) reflects the differences in the amount of rainfall that occurred during the months. But as Farrow (1975) reported for *Locusta migratoria migratorioides*, nymphs once hatched continue developing irrespective of the condition of the vegetation in their surrounding. This explains why there was no significant difference in density between the habitats. *L. migratoria migratorioides* is an oedipodine and most of the species whose nymphs were observed during dry seasons were also oedipodines, namely, *A. patruelis*, *A. longipes*, *G. verticalis*, *A. thalassinus*, *S. savignyi* and *A. ndoloi*. In semi-arid parts of Cyprus *Dociostaurus moroccanus*, which is a gomphocerine, lays eggs that do not hatch until the environmental conditions are favourable for nymphal development (Dempster, 1957). During the present study nymphs of two gomphocerine species, *P. squalus* and *A. brevipennis* were seen only after the rains had started and the vegetation was fresh and green.

The difference between habitats and also between months with respect to adult densities were significant ($P < 0.05$). There was an increase in adult density with the emergence of the adults from the nymphs. Many factors may account for the reduction in density of adults during dry periods but two which came to light during this study were migration in the case of *O. instillatus* at Luai and hiding in soil cracks in the case of *A. thalassimus* and *T. cunctator* at Gatab. Those in hiding would come to the surface when the rains came. This observation supports Joyce (1952) who found that *A. simulatrix* hid in the soil cracks during the dry season.

5.2.5 Acridid biomass

Mean live and oven-dry weights of females, males and nymphs were higher at higher elevations and therefore sites with higher expected mean annual precipitation (EMAP) (Table 6). Biomass of nymphs and adults differed significantly between months and between habitats ($P < 0.05$) (Table 9).

Table 6

Mean live and oven-dry weights (g) of females, males and nymphs of various species drawn from each of the three study sites

	Gatab		Luai		Balessa Kulal	
	live weight	oven-dry weight	live weight	oven-dry weight	live weight	oven-dry weight
Females	1.60(19)*	0.40(19)	1.00(25)	0.25(25)	0.66(15)	0.17(15)
Males	0.72 (19)	0.15(19)	0.47(24)	0.09(24)	0.33(15)	0.06(15)
Nymphs	0.31(12)	0.05(12)	0.18(12)	0.03(12)	0.11(6)	0.01(6)

* Figures in parenthesis represent the number of species from which the weighed individuals were drawn

Table 7

Monthly live acridid biomass (g m^{-2}) for nymphs and adults at each study site 1979-1980

Month	Biomass (g m^{-2}) at the study sites					
	Gatab		Luai		Balessa Kulal	
	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults
Nov	0.0070	0.2720	0.0040	0.1570	0.0001	0.0060
Dec	0.0070	0.0650	0.0030	0.0820	0.0010	0.0060
Jan	0.0080	0.0500	0.0030	0.0330	0.0010	0.0050
Mar	0.0030	0.0650	0.0010	0.0260	0.0002	0.0070
Apr	0.0010	0.0990	0.0020	0.0470	0	0.0040
May	0.0060	0.1520	0.0160	0.0270	0.0010	0.0050
June	0.0110	0.1110	0.0110	0.1100	0.0010	0.0260
July	0.0280	0.1990	0.0130	0.1550	0.0020	0.0660
Aug	0.0030	0.1260	0.0010	0.1110	0.0010	0.0200
Sept	0.0010	0.1700	0.0100	0.0570	0.0003	0.0140
Oct	0.0030	0.0880	0.0003	0.0380	-	-

Table 8

Monthly acridid biomass (g m^{-2}) of nymphs and adults at each habitat 1979-1980

Months and developmental stages		Habitat								
		1*	2	3	4	5	6	7	8	9
Nov	Nymphs	0.010	0.003	0.002	0.002	0.007	0	0.000	0	0
	Adults	0.377	0.166	0.292	0.092	0.088	0.003	0.010	0.008	0.002
Dec	Nymphs	0.012	0.001	0.002	0.003	0.003	0	0.001	0.000	0
	Adults	0.060	0.079	0.113	0.096	0.036	0.004	0.006	0.009	0.003
Jan	Nymphs	0.009	0.006	0.002	0.002	0.004	0	0.001	0	0.001
	Adults	0.033	0.066	0.045	0.029	0.025	0.002	0.004	0.011	0.004
Mar	Nymphs	0.004	0.001	0.000	0.001	0.000	0	0.000	0.000	0
	Adults	0.073	0.057	0.026	0.031	0.021	0.002	0.006	0.010	0.008
Apr	Nymphs	0.001	0.001	0.002	0.002	0.001	0	0	0	0.002
	Adults	0.118	0.079	0.062	0.025	0.053	0.003	0.008	0.004	0.002
May	Nymphs	0.005	0.006	0.001	0.037	0.010	0.002	0.000	0.001	0.001
	Adults	0.121	0.177	0.029	0.028	0.025	0.006	0.007	0.003	0.005
June	Nymphs	0.014	0.007	0.010	0.001	0.023	0	0.000	0.001	0
	Adults	0.146	0.076	0.077	0.156	0.097	0.042	0.019	0.027	0.015
July	Nymphs	0.012	0.034	0.013	0	0	0.001	0.003	0.001	0
	Adults	0.310	0.087	0.163	0.209	0.094	0.092	0.064	0.067	0.042
Aug	Nymphs	0.005	0.001	0	0	0.001	0.000	0.001	0.001	0.000
	Adults	0.168	0.084	0.174	0.105	0.054	0.026	0.025	0.018	0.009
Sept	Nymphs	0.001	0.001	0	0	0.001	0	0.000	0.000	0.000
	Adults	0.186	0.154	0.066	0.068	0.037	0.010	0.017	0.020	0.080

* Key

1 - Upper Gatab habitat
2 - Lower Gatab habitat
3 - Luai enclosure habitat
4 - Luai grazed habitat
5 - Luai *A. etbaica* habitat
6 - Balessa Kulal lava habitat
7 - Balessa Kulal enclosure habitat
8 - Balessa Kulal sand river bed habitat
9 - Balessa Kulal *A. reficiens* habitat

Table 9

Double-classification analysis of variance for biomass of acridid nymphs and adults at nine habitats during ten months

(a) Nymphs

Source of variation	SS	df	MSS	F
Between habitats	0.221	8	0.0276	13.8*
Between months	0.0984	9	0.0109	5.45*
Error	0.147	72	0.0020	
Total	0.4664	89		

(b) Adults

Source of variation	SS	df	MSS	F
Between habitats	0.00075	8	0.000094	2.85*
Between months	0.00066	9	0.000073	2.21*
Error	0.00234	72	0.000033	
Total	0.00375	89		

*Significant difference at $P < 0.05$

5.2.6 Discussion

The mean live and mean oven-dry weights of females, males and nymphs, in a sense obeyed Bergman's rule (Moen, 1973). Individuals from higher and wetter Gatab on Mt. Kulal were the heaviest while those from hot Balessa Kulal were the lightest. There was strong evidence of significant positive relationship between mean live weights and altitude and mean oven-dry weights and altitude ($r_1 = 0.99$; r calculated by product moment method according to Campbell (1975).

There was also a significant relationship between EMAP and mean oven-dry weight of females, males and nymphs; and between EMAP and mean live weight of nymphs ($r_1 = 0.09$). A high significant positive relationship was also observed between EMAP and mean female live weight ($r_1 = 0.98$) and mean males live weight ($r_1 = 0.99$). These data indicate that colder and wetter places support heavier acridid fauna than do lower, hotter and drier places.

Elevation differences between the times when biomass of acridids reached a peak after April rains corresponded to those for density in May, June, July for Gatab, Luai and Balessa Kulal respectively. The differences were presumably determined by the amount of rainfall received by each site and this in turn caused growth of fresh vegetation on which acridids fed. That acridids are particularly sensitive to ecological changes in their habitat, particularly vegetation, has been mentioned by Uvarov (1957) and Hemming (1966).

Live wieghts of acridids in the study sites have been emphasized because the acridids were compared with large domestic herbivores as reported by Field (1979).

The biomass of nymphs and of adults differed significantly between months and between habitats ($P < 0.05$). The main factor underlying all these is that different habitats and months receive variable amounts of rainfall. This in turn means that the quality of vegetation varies from habitat to habitat and from month to month and so does acridid biomass. Gillon and Gillon (1973) demonstrated that arthropod biomass was four times larger during the rains then during dry periods. In this investigation there was an increase in total biomass ($g\ m^{-2}$) some time after the rains and not during the rains. This may be explained by the fact that the present investigation was carried out in an area which experienced very long dry spells (3-5 months) and therefore some time was ncessary before biomass reached a peak.

5.2.7 Sex ratio

The results (Table 10) show that for most species of acridids females occur in significantly higher numbers than males.

Table 10

The number of males and females of 17 species of acridids caught in the study sites and the significance of the difference between them

Species	Number of Individuals		Difference and signficance
	Females	Males	
C. homalodemus	51	21	30*
P. purpurascens	24	37	13[a]
P. kulalensis	84	41	43*
P. conica	75	56	19[a]
A. glaucopsis	50	40	10[a]
E. plorans	66	11	55*
C. fuscocoeruleipes	30	45	15[a]
P. decoratus	57	21	36*
C. tatarica	27	20	7[a]
Odontomelus sp.	101	41	60*
A. thalassinus	78	50	18*
S. savignyi	53	48	5[a]
G. verticalis	23	108	85*
M. fasciata	43	23	20*
A. longipes	75	39	36*
A. patruelis	96	37	59*
P. squalus	40	43	3[a]

Key

* = significant $P < 0.05$

a = non-significant $P > 0.05$

5.2.8 Discussion

Although females generally occurred in larger numbers than males, in one species, *G. verticalis*, the number of males was significantly higher than the number of females. The males of this species were more active and easy to catch and this may be the reason for their apparent larger numbers. On the other hand closely related oedipodines, namely, *A. longipes, A. patruelis, A. thalassinus* and *M. fasciata* showed a greater number of females than males. The difference between the number of females and males of *S. savignyi* was not significant. Dempster (1957) attributed the higher numbers of one sex over the other to superactivity which made individuals of such a sex easily disturbed, seen, followed and caught. This was the case in the present study with males of *G. verticalis*, females of *A. thalassinus*, *P. decoratus*, and *A. patruelis*. Dempster's superactivity hypothesis did not work in *P. kulalensis* and *Odontomelus* sp. whose males, although more active than females were not caught in significantly higher numbers than females. It seems therefore that all factors being the same superactivity of the sex of an acridid species must be coupled with some opitimum density in order that they be easily seen and caught.

Farrow (1975) found a higher number of males than females in *L. migratoria migratorioides* and attributed this to the fact that males were perhaps easier to catch in the field than females. Both *L. migratoria migratorioides* and *G. verticalis* are oedipodines and in both cases males are more numerous than females.

The tendency of one of the sexes to occur in significantly higher numbers than the other is found in members of both primitive and advanced subfamilies and is not related to any taxonomic order.

5.2.9 Dynamics of developmental stages

The calculated percentages for various categories of developmental stages during eight months for all three study sites (Tables 11 and 12) show that on the whole over 30% of the species examined from all the sites occurred as adults only. No gravid females or nymphs were recorded from this 30% of species.

No gravid females or nymphs were recorded from this 30% of species.

The percentage of gravid species reduced as the dry season continued while the percentage of those species with nymphs continued to rise even during the dry season. However this does not appear to be the case at the more arid Balessa Kulal, particularly after November rains. Here the percentage level of the gravid species and of those with nymphs remained more or less the same.

Long drought hit the acridids more in those sites with higher EMAP. Thus, even at the peaks of the dry season, nymphs of certain species still occurred at Balessa Kulal which has the least EMAP of 100-200 mm. Two such acridid species were *L. aethiopica* and *P. conica* in September 1980.

Table 11

Percentages of categories of developmental stages of acridids caught and the average rainfall (mm) for the three study sites combined

	Months							
	Dec	Jan	Mar	Apr	May	July	Aug	Sept
Number of species examined	43	43	29	28	29	35	17	27
Percentage of species that occurred as adults only	44	37	59	50	31	34	35	78
Percentage of species with nymphs	23	32	37	18	34	54	65	22
Percentage of species that were gravid	32	12	11	36	38	20	0	0
Percentage of species with nymphs and gravid females	12	5	7	4	7	6	0	0
Average amount of rainfall (mm)	45.1	7.0	4.6	88.3	68.2	0.5	0	0

Table 12

Percentages of categories of developmental stages of acridids caught and the average rainfall (mm) for each of the three study sites

	Months							
	Dec	Jan	Mar	Apr	May	July	Aug	Sept
Number of species examined								
Gatab	15	15	15	16	13	17	12	11
Luai	15	11	9	12	12	14	10	11
Balessa Kulal	8	9	9	7	7	8	10	11
% of species that occurred as adults only								
Gatab	20	13	33	38	23	24	17	45
Luai	60	64	67	67	33	36	60	100
Balessa Kulal	63	78	78	33	43	38	68	82
% of species with nymphs								
Gatab	33	67	40	25	31	53	83	36
Luai	27	55	44	17	17	50	40	0
Balessa Kulal	44	11	11	0	43	50	30	18
% of species with gravid females								
Gatab	73	20	13	50	54	18	0	0
Luai	40	18	11	8	42	29	0	0
Balessa Kulal	38	11	11	33	14	13	0	0
% of species with nymphs and gravid females								
Gatab	13	13	7	6	8	6	0	0
Luai	13	9	11	0	0	14	0	0
Balessa Kulal	13	0	0	0	0	13	0	0
Average amount of rainfall (mm)								
Gatab	99.7	6.6	4.2	150.7	86.7	0	0.2	0
Luai	28	13	8	69	65	0	0	5.0
Balessa Kulal	7.6	1.3	6.6	45.3	52.8	0	0	0

5.2.10 Discussion

The power of egg production in acridids reduces as food quality lowers (McCaffery, 1975; Lee and Wong, 1978). Although the percentage of species with nymphs rose when that of those that were gravid fell during dry periods at Gatab and at Luai, it was not the same thing at Balessa Kulal particularly during the months of December and January. The percentage level of the gravid species and of those with nymphs remained more or less the same at Balessa Kulal during these two months (Table 12). A possible explanation of this is that female adults of acridid species here must make use of the new plant growth for egg production while nymphs hatched from eggs previously laid must also depend on this short-lived fresh plant food material. Balessa Kulal is the most arid of all the three sites and so the acridids there must make maximum use of any favourable opportunity.

There appeared to be some delay before individuals of species became gravid after the rains of April in the sites with more rainfall. At Balessa Kulal, on the other hand the gravid condition appeared with the onset of April rains (Table 12). Joyce (1952) reported a similar situation in the *Geophileus* acridid species in East Central Sudan which bred with the onset of rains.

The higher percentage of gravid females at Gatab in December 1979 than in May 1980 helps to explain the occurrence of a higher density of nymphs in January 1980 than in May 1980 at this site (Table 3).

Although no endophytic oviposition was observed during this study it has been reported in such insects as the Mediterranean fruitfly *Ceratitis capitata* Wied (Abasa, 1972), *Chrysochraon dispar* (Ramme, 1926), *Gesonula punctifrons* (Sankaran et al., 1966); and in *Orbillus coeruleus* Chapman (1961) reported epiphytic oviposition.

5.2.11 Niche overlap

Niche breadth and overlap values of ten common acridid species and their relative interactions (Tables 13,14 and 15) show that *A. longipes* has the highest niche breadth value. Species occurring in more habitats than the others have higher niche overlap values than those they may occur with together, at least, at a habitat. *A. patruelis* had the highest relative interaction values while *A. pulla* had the least relative interaction of all the ten acridid species.

The two oedipodines, *A. longipes* and *S. savignyi*, which occurred in all habitats at Balessa Kulal had the highest niche breadth values. The other oedipodines, *A. patruelis, A. thalassinus* and *G. verticalis* which occurred only at Lower and Upper Gatab habitats had the lowest niche breadth values. *A. longipes* also occurred at all the three habitats of Luai.

Table 14 shows that, in general, the species with higher niche breadth values also have greater niche overlap values and that such species do overlap over opposite members, of their pair, which have lower niche breadth values. This is what was found in the case of *Odontomelus* sp. (1.07) and *G. verticalis* (0.55). The former species avoided competition for habitat with the latter by being able to colonise more habitats. The competition between these two species for habitat was therefore not intense. Intense competition occurred between *A. thalassinus* (0.93) and *A. patruelis* (1.07) and between *P. kulalensis* (0.85) and *Odontomelus* sp. (0.95).

Although *A. patruelis* occurred mainly in the Lower Gatab habitat and along certain paths leading to the forest through Upper Gatab and although it had only four contiguous species, *A. thalassinus, G. verticalis, P. kulalensis* and *Odontomelus* sp., it still showed the highest relative interaction values.

Table 13

Niche breadth values
of ten acridid species drawn from all the three study sites

Species	Niche breadth values
A. longipes	6.54
S. savignyi	3.74
P. conica	3.42
A. pulla	3.09
Odontomelus sp	2.52
P. kulalensis	2.24
A. ndoloi	2.14
A. patruelis	1.63
A. thalassinus	1.42
G. verticalis	1.29

Table 14

Possible pairs of ten common acridid
species with their corresponding niche overlaps

P. kulalensis	1.23	and	*A. thalassinus*	0.78
P. kulalensis	1.16	and	*A. patruelis*	0.84
P. kulalensis	0.61	and	*G. verticalis*	0.34
P. kulalensis	0.85	and	*Odontomelus* sp.	0.95
P. kulalensis	0.06	and	*A. longipes*	0.17
P. kulalensis	0.17	and	*A. ndoloi*	0.17
P. kulalensis	0.12	and	*A. pulla*	0.16
P. conica	0.76	and	*S. savignyi*	0.04
P. conica	0.03	and	*A. pulla*	0.03
P. conica	0.76	and	*A. longipes*	1.45
Odontomelus sp.	1.13	and	*A. patruelis*	0.73
Odontomelus sp.	1.14	and	*A. thalassinus*	0.64
Odontomelus sp.	1.07	and	*G. verticalis*	0.55
Odontomelus sp.	0.12	and	*A. ndoloi*	0.10
Odontomelus sp.	0.04	and	*A. longipes*	0.10
Odontomelus sp.	0.12	and	*A. pulla*	0.14

(Table 14 contd.)

A. pulla	1.00	and	*A. ndoloi*	0.69
A. pulla	0.41	and	*A. longipes*	0.88
A. pulla	0.04	and	*S. savignyi*	0.04
A. thalassinus	0.93	and	*A. patruelis*	1.07
A. thalassinus	0.37	and	*G. verticalis*	0.34
S. savignyi	0.54	and	*A. longipes*	0.97
G. verticalis	0.42	and	*A. patruelis*	0.53
A. longipes	1.04	and	*A. ndoloi*	0.34

Table 15

Relative interaction values of ten common acridid species

Species	Number of contiguous species	Relative interaction values
A. patruelis	4	0.79
A. longipes	6	0.77
A. thalassinus	4	0.68
Odontomelus sp.	7	0.65
P. kulalensis	7	0.60
P. conica	3	0.52
S. savignyi	3	0.47
G. verticalis	4	0.33
A. ndoloi	4	0.33
A. pulla	6	0.30

5.2.12 Discussion

The first three species with the highest niche breadth values, namely, *A. longipes* (6.54), *S. savignyi* (3.74) and *P. conica* (3.42), were inhabitants of the more arid Balessa Kulal while the last three species, *A. patruelis* (1.63), *A. thalassinus* (1.42) and *G. verticalis* (1.29) occurred only in the least arid Gatab on Mt. Kulal.

This may be explained by the fact that the species inhabiting the arid areas, with limited resources in terms of food, may explore more habitats than those which dwell in the less arid environments. The latter have adopted a specialist approach with regards to habitat selection while the former are generalists in this regard. This parallels what Rowell (1978) found in connection with feeding behaviour of acridids in Costa Rican forest. These acridids, with plenty of food around were found to have adopted a specialist approach to feeding by each species feeding only on selected plant species.

That *A. patruelis* had the highest relative interaction values of all the ten common acridid species was due to its usually very high density coupled with high densities of its contiguous species.

5.3 Acridid feeding behaviour

5.3.1 Mandibular structure

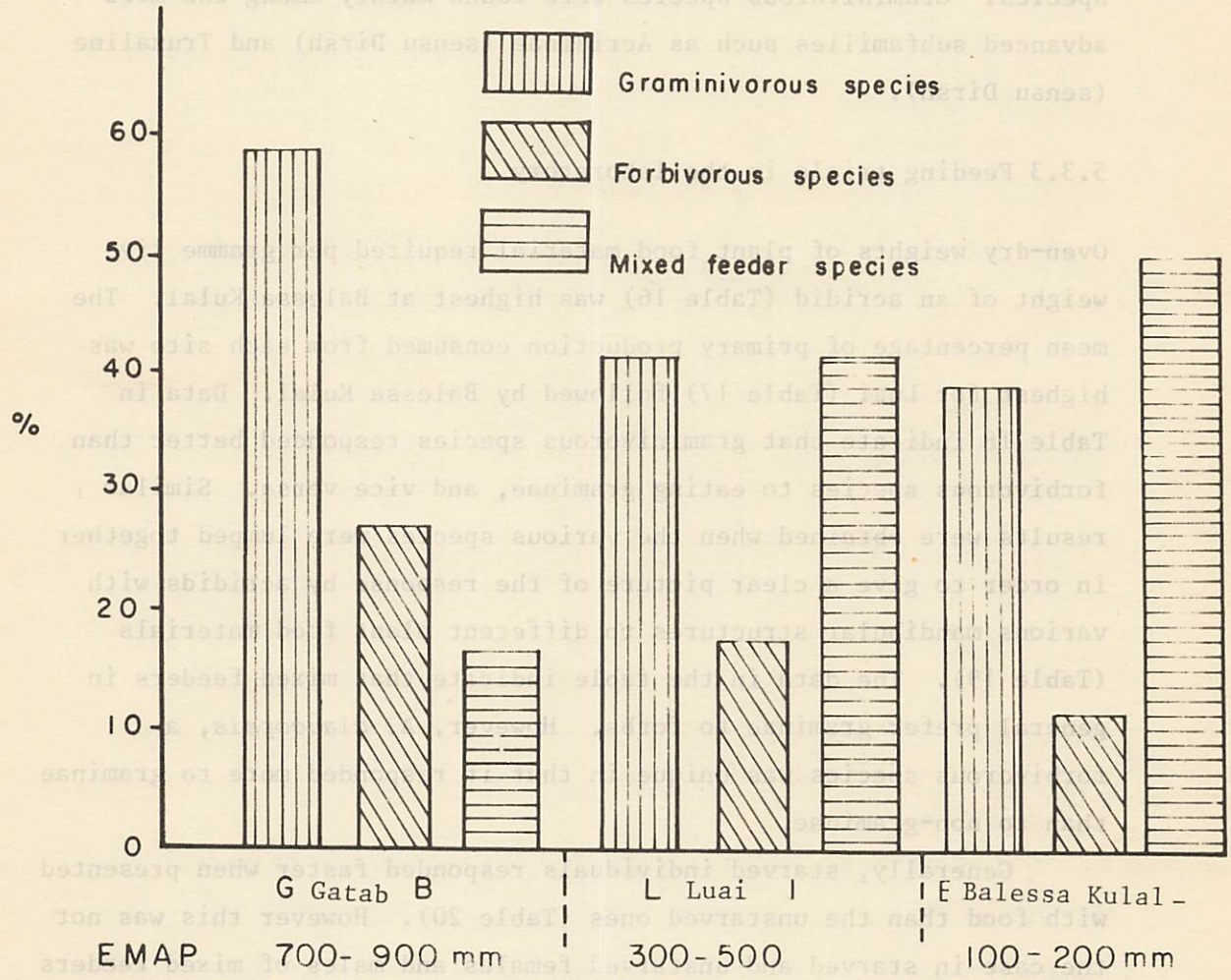
Mandibles were examined in 19 species from Gatab, 22 species from Luai and 18 species from Balessa Kulal. Each species was classified as graminivorous, forbivorous or a mixed feeder. The relative distribution, in percentages of various mandibular structural adaptations to feeding in the three study sites (Fig 3), indicates that the percentage of the graminivorous and forbivorous species falls in more arid sites as the percentage of mixed feeders rises. The percentages of graminivorous species were considerably higher than those of forbivorous species at all the three sites (Fig 3).

5.3.2 Discussion

Acridids living in semi-arid areas such as Balessa Kulal should be able to eat either graminae or non-graminae, whichever is available. It may be for this reason that the percentages of mixed feeders falls as altitude, and therefore EMAP, rises.

Most of the graminivorous species belong to the advanced subfamilies of Acrididae and this is evidence that graminae may be more recent in evolutionary terms than most of the non-graminae.

Fig. 3 Relative distribution of mandibular structures within the study area.



That the percentage of graminivorous species is higher than that of forbivorous species at each site points to the fact that in this area there may be more advanced acridid species than less advanced ones.

Though adaptation of mandibular structure to feeding does not seem to be connected with the taxonomic position of an acridid species, it became clear from this study that the primitive subfamily of Pyrgomorphinae comprised of mainly forbivorous species. Graminivorous species were found mainly among the more advanced subfamilies such as Acridinae (sensu Dirsh) and Truxaline (sensu Dirsh).

5.3.3 Feeding trials in the laboratory

Oven-dry weights of plant food material required per gramme live weight of an acridid (Table 16) was highest at Balessa Kulal. The mean percentage of primary production consumed from each site was highest for Luai (Table 17) followed by Balessa Kulal. Data in Table 18 indicate that graminivorous species responded better than forbivorous species to eating graminae, and vice versa. Similar results were obtained when the various species were lumped together in order to give a clear picture of the response by acridids with various mandibular structures to different plant food materials (Table 19). The data in the table indicate that mixed feeders in general prefer graminae to forbs. However, *A. glaucopsis*, a forbivorous species was unique in that it responded more to graminae than to non-graminae.

Generally, starved individuals responded faster when presented with food than the unstarved ones (Table 20). However this was not the case in starved and unstarved females and males of mixed feeders given graminae. Unstarved individuals responded faster. Graminivorous and forbivorous species responded faster to graminae and to non-graminae respectively under both starved and unstarved conditions. But there did not seem to be any difference in the rate of response to graminae and non-graminae by the nymphs of forbivorous species.

Adults of mixed feeders responded faster to graminae than to non-graminae.

The majority of the most preferred plant species were graminae (Table 21). Only *Brassica oleracea* and *Salvadora persica* were the non-graminae among the top ten preferred plant species.

Table 16

Oven-dry weights (g) of food required per gramme live weight of acridids

Period	Oven-dry weight per live weight in grammes		
	Sites		
	Gatab	Luai	Balessa Kulal
Nov Dec 1979	0.15	0.11	0.15
Jan Mar 1980	0.10	0.10	0.12
Apr May 1980	0.13	0.11	0.16
June, July and Aug 1980	0.11	0.16	0.12
Overall average	0.12	0.12	0.14

Table 17

Food intake (g m^{-2} d^{-1}) and percentage of primary production consumed by 23 most common acridid species in the study area

Period	g m^{-2} d^{-1} and percentage of primary production consumed by acridids		
	Sites		
	Gatab	Luai	Balessa Kulal
Nov Dec 1979	0.021 (1.3*)	0.012 (2.7)	0.002 (1.3)
Jan Mar 1980	0.004 (0.3)	0.003 (0.7)	0.001 (0.6)
Apr May 1980	0.012 (0.8)	0.010 (2.3)	0.002 (1.3)
June, July and Aug 1980	0.012 (0.8)	0.031 (7)	0.011 (6.9)
Mean ($\bar{x}$)	0.012 (0.8)	0.014 (3.2)	0.004 (2.5)

Mean for all sites combined = 0.01 10 kg km^{-2} d^{-1} which is 2.17% of primary production.

*Figures in parentheses represent percentage of primary production consumed by acridids.

Table 18

The percentage of acridids that fed on graminae and non-graminae

Acridid species	Mandibular Structure	Graminae			Non-graminae		
		No. of plant species presented	No. of presentations	% fed	No. of plant species presented	No. of presentations	% fed
A. thalassinus	G*	6	45	96	9	58	34
A. patruelis	G	5	28	75	11	18	17
Odontomelus sp	G	5	48	90	9	38	21
A. brevipennis	G	7	19	95	8	15	0
P. squalus	G	6	27	96	12	21	10
P. galinieri	G	6	17	59	5	7	57
G. verticalis	G	6	16	75	6	36	42
D. griseus	F	3	5	0	18	62	76
A. glaucopsis	F	5	13	85	13	23	74
A. ornatipes	F	2	3	33	7	10	40
P. decoratus	F	6	12	50	10	16	81
P. conica	F	5	8	38	12	19	58
A. longipes	MF	9	44	80	20	81	51
H. coerulescens	MF	6	11	91	13	27	85
C. homalodemus	MF	9	92	43	25	122	63
S. savignyi	MF	5	13	62	21	42	64
S. turkanae	MF	5	8	80	11	32	56
A. ruficornis	MF	2	5	80	9	18	72
C. fuscocoeruleipes	MF	4	16	93	8	15	73
E. plorans	MF	3	12	58	10	26	62
A. pulla	MF	3	8	63	7	9	78
C. tatarica	MF	4	18	89	9	13	91
O. installatus	MF	4	11	91	6	11	36
Mean % fed				71			55

G* = graminivorous species

F = forbivorous species

MF = mixed feeder

Table 19

The percentage of acridid species with mandibular structural adaptations that fed on graminae and non-graminae

Mandibular structure	Graminae			Non-graminae		
	Number of acridid species tried	Food presentations	% fed	Number of acridid species tried	Food presentations	% fed
Graminivorous	7	246	88	7	153	26
Forbivorous	5	48	52	5	160	86
Mixed feeder	11	187	71	11	416	65

Table 20

Approximate rate of response to presented food (in minutes)

		Females				Males				Nymphs			
		a*	p	b	e	a	p	b	e	a	p	b	e
Sgg*	G*	29	66	109	115	37	52	128	136	33	65	82	86
	F	73	113	180	189	26	86	99	108	40	198	216	220
	MF	50	117	210	212	81	135	216	224	148	171	198	233
Sgn	G	87	179	216	224	31	179	246	252	31	98	120	123
	F	46	106	140	144	44	76	89	94	56	180	210	215
	M	54	115	226	234	156	188	264	269	58	74	218	238
Ugg	G	65.	99	133	139	68	105	161	175	54	61	155	159
	F	108	115	182	194	61	139	278	283	47	210	230	238
	MF	78	125	183	208	101	145	181	187	189	245	333	342
Ugn	G	135	172	357	362	83	142	294	303	60	179	294	320
	F	58	93	144	149	5	95	105	112	69	193	235	245
	MF	164	230	319	327	145	251	404	413	128	204	279	286

*Key: a= approaching; p = probing; b = biting; e = eating; G = graminivorous species; F = forbivorous species; MF = mixed feeder species; Sgg = starved given graminae; Ugg = unstarved given graminae; Sgn = starved given non-graminae Ugn = unstarved given non-graminae.

Table 21

Plant species preference by 23 acridid species tested combined

Plant species	Number of presentations	% preference
Pennisetum mezianum	8	100
Brachiaria serrata	14	93
Zea mays	36	92
Salvadora persica	43	86
Brassica oleracea	42	83
Digitaria scalarum	158	82
Panicum maximum	14	79
Dichanthium insculptum	94	74
Tricholaena teneriffae	15	73
Saccharum officinarum	36	72
Sericocomopsis hildebrandti	21	71
Commelina benghalensis	21	71
Lycopersicon esculentum	16	69
Themeda triandra	94	67
Crinum kirkii	17	65
Acacia drepanolobium	11	64
Cajanus cajan	27	63
Solanum incanum	28	57
Ipomea batatas	43	56
Euclea divinorum	55	53
Rhus natalensis	39	51
Rhus vulgaris	42	50
Duosperma eremophilum	37	49
Acacia nilotica	50	48
Juniperus procera	23	48
Aspilia mossambiciensis	90	46
Carissa edulis	28	43
Osyris abyssinica	23	39
Heliotropium albohispidum	16	38
Hypoestes aristata	15	27
Plectranthus igniarius	17	6

5.3.4 Discussion

From the results in Table 16 it is concluded that smaller acridids require more food per unit live body weight than larger ones. This is demonstrated by the results from Balessa Kulal where individual acridids are smaller than those at the other two study sites (Table 6).

On the average for the whole study area, acridids eat food that is equivalent to about 13% of their body weight per day. However, wide variations occurred between species and between sexes where smaller species and males ate more relative to their body weights than did larger species and females respectively.

Estimates of primary production at the three study sites taken during the rainy months (April and November) of 1976, 1977 and 1978 were 1.56 g m^{-2} d^{-1} for Gatab, 0.44 g m^{-2} d^{-1} for Luai and 0.16 g m^{-2} d^{-1} for Balessa Kulal and there has not been much difference since then (Herlocker, personal communication). Based on this report the mean percentage of 2.17% of primary production consumed by acridids from all the study sites combined was lower than that of 7% calculated for camels, sheep and goats combined (Field, 1979). Luai had the highest percentage of 3.2% of primary production consumed by acridids. White (1978) reported that no more than 6% of primary production is consumed by acridids and that in the majority of grasslands their consumption is unlikely to exceed 1 - 2%.

A. glaucopsis, a forbivorous species responded more successfully to graminae than to non-graminae (Table 18). However, it ate mainly the grass stems. The data in Table 19 indicate that mixed feeders generally prefer graminae to non-graminae.

From the mean percentages, it appears that in general acridids in the IPAL study area prefer grasses to forbs (Table 18). The unstarved mixed feeders were also shown to respond faster to graminae than the starved ones and it therefore appears that there is some element in grass that the acridids require most of the time to supplement their diet. Further, adults of mixed feeders responded faster to graminae than to forbs (Table 20).

Only two non-graminae, *B. oleracea* and *S. persica* (Table 21) were among the top ten preferred plant species. There was a strong preference for maize (*Zea mays*), a graminaceous plant. That acridids do well on this particular plant was demonstrated in the acridid *Oxya japonica* by Lee and Wong (1978).

Of the six cultivated crops *Ipomea batatas* was least preferred. This could have been due to the presence of groups of alkaloids (Hanzen, 1975) which inhibit feeding. Nonetheless, the six crops were among the top twenty preferred plants. Any attempt, therefore, to introduce some subsistence farming in the Mt. Kulal area should take into account the possibility of some of the acridid species becoming serious pests of these crops.

D. insculptum, *T. teneriffae* and *S. officinarum* are the three least preferred graminae species (Table 21). The slight aromatic scent of *D. insculptum* may be the reason for its low index of preference. The other two grasses have hard leaves. Acridids avoid eating certain plant species due to the chemical composition or physical nature of such plant species (Bernays et al., 1974; Bernays and Chapman, 1970, 1977; Adams and Bernays, 1978; Woodhead and Bernays, 1978). In this study a forb, *P. igniarius*, a strongly scented labiate, was hardly ever bitten let alone eaten.

5.3.5 Actual plant species observed being eaten in the field

Data on the acridid species, the plant and part of the plant on which it fed (Table 22) indicate that quite often it was the leaves of the plants that were eaten, rarely were other parts eaten. More observations were made on *D. griseus* than on any other species and this was due to the fact that this large short-winged species is sluggish and rarely disturbed by the presence of a human being in the vicinity. For this reason it could be easily located, approached and observed. Forbivorous, graminivorous and mixed feeders were observed in the field eating forbs, grasses and forbs and grasses respectively.

Table 22

Acridid species, plant and part of the plant on which they fed in various study sites

Acridid species	Number observed	Species of plant	Part eaten	Study site
D. griseus	5	*B. abyssinica*	leaves	Gatab
D. griseus	4	*C. kirkii*	leaves	Gatab
D. griseus	2	*A. mossamibiciensis*	leaves	Gatab
D. griseus	3	*I. batatas*	leaves	Gatab
D. griseus	7	*B. oleracea*	leaves	Gatab
P. conica	2	*S. hildebrandti*	leaves	Balessa Kulal
H. rantae	2	*S. persica*	leaves	Balessa Kulal
C. tatarica	4	*B. serrata*	leaves	Luai
M. fasciata	10	*D. scalarum*	leaves	Gatab
A. patruelis	8	*D. scalarum*	leaves	Gatab
A. ndoloi	3	*B. serrata*	leaves	Luai
A. longipes	2	*I. spinosa*	bark	Balessa Kulal
A. thalassinus	7	*D. scalarum*	leaves	Gatab
P. purpurascens	4	*I. batatas*	leaves	Gatab
P. purpurascens	3	*B. oleacea*	leaves	Gatab

Although one acridid species, *A. glaucopsis*, was shown in the laboratory to prefer stems of grasses, the fact that acridids observed feeding in the field fed mainly on leaves is important. Leaves are the site of photosynthesis and feeding on them may greatly affect this process and reduce the capacity of primary production. This may be more so in cases of some major outbreaks of certain acridid species such as was the case in Soysambu pastures in the Rift Valley of Kenya (Le Pelley, 1952). *A. longipes* ate the live bark of *I. spinosa* perhaps because during this time (January 1980) there were no leaves on this plant at one of the grazed parts in the Balessa Kulal enclosure habitat.

5.3.6 Times of active feeding

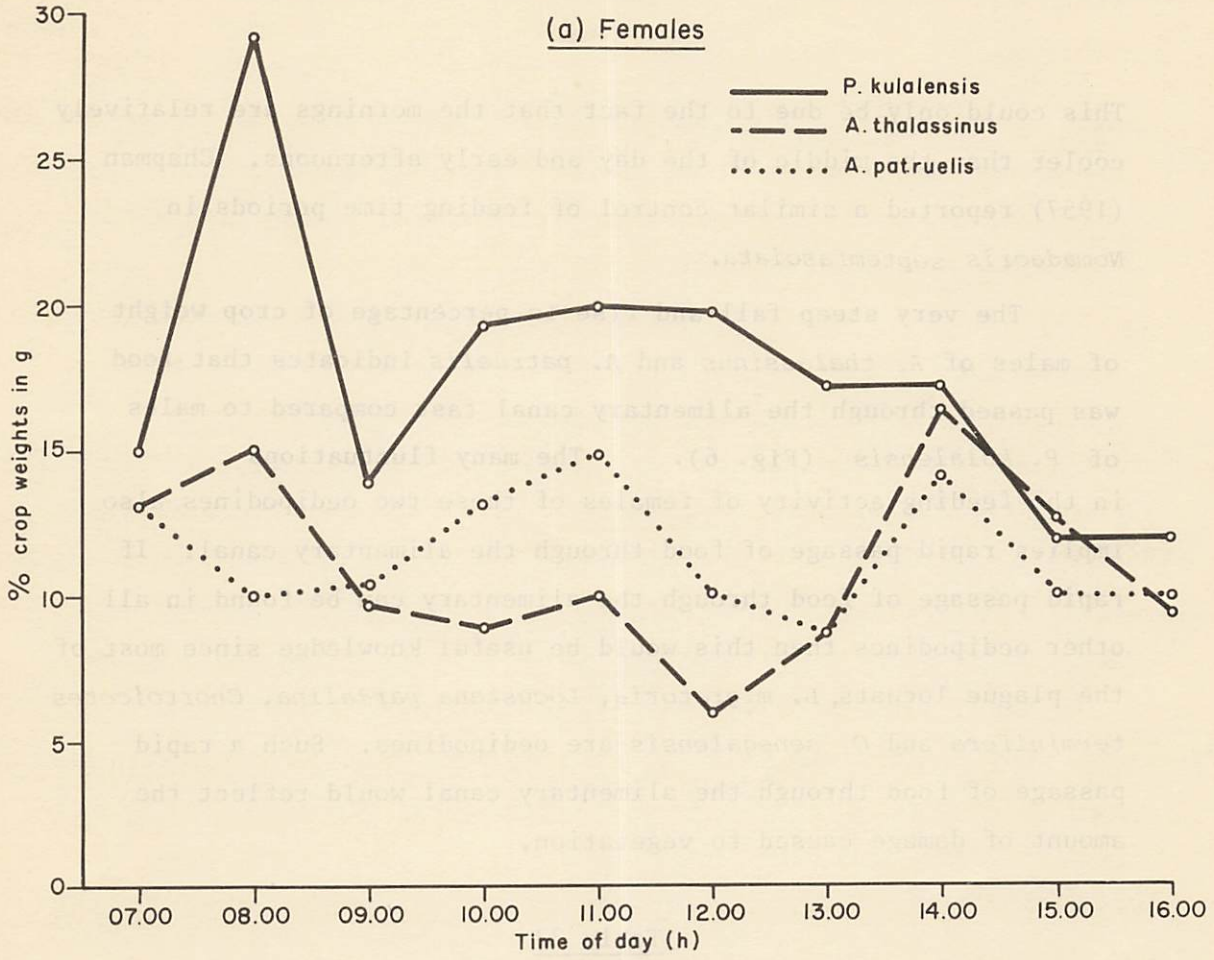
Mean percentage crop weights of females and males of three acridid species (Fig 4) indicate that there are differences in the time of active feeding between seasons and between sexes. The feeding activity pattern was similar during both seasons and in both sexes of the oedipodines observed, *A. thalassinus, A. patruelis, G. verticalis, A. longipes, A. ndoloi, O. senegalensis* and *M. fasciata* (Table 23), except in females of *G. verticalis* and males of *A. patruelis*. In general the feeding in this subfamily was highest around noon. Males of *G. verticalis* had no specific feeding time period during the dry season.

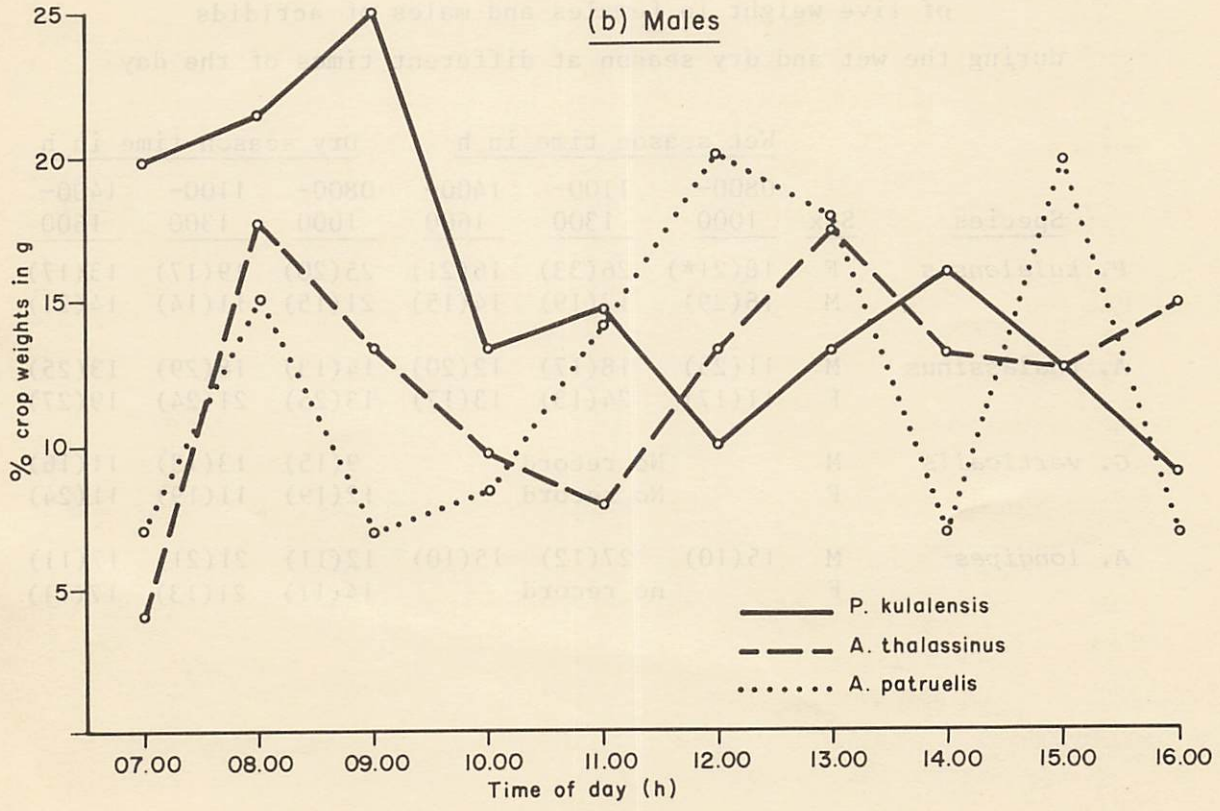
5.3.7 Discussion

That males of *G. verticalis* had no specific feeding period during the dry season (Table 23) may be explained by the fact that during this period food was in short supply and of poor quality. Selecting a particular feeding time period would therefore not benefit them.

In the only pyrgomorphine, *P. kulalensis*, observed (Table 23) each sex had its own feeding pattern that was constant during the two season . Females fed in the morning and at noon, while males fed actively in the morning, were less active at noon and only fed slightly in the afternoon.

Fig. 4. Percentage crop weights in g of females and males of 3 acridid species





This could only be due to the fact that the mornings are relatively cooler than the middle of the day and early afternoons. Chapman (1957) reported a similar control of feeding time periods in *Nomadacris septemfasciata*.

The very steep fall and rise in percentage of crop weight of males of *A. thalassinus* and *A. patruelis* indicates that food was passed through the alimentary canal fast compared to males of *P. kulalensis* (Fig. 6). The many fluctuations in the feeding activity of females of these two oedipodines also implies rapid passage of food through the alimentary canal. If rapid passage of food through the alimentary can be found in all other oedipodines then this would be useful knowledge since most of the plague locusts, *L. migratoria*, *Locustana pardalina*, *Chortoicetes terminifera* and *O. senegalensis* are oedipodines. Such a rapid passage of food through the alimentary canal would reflect the amount of damage caused to vegetation.

Table 23

Mean values of crop weight as a percentage of live weight in females and males of acridids during the wet and dry season at different times of the day

		Wet season time in h			Dry season time in h		
Species	Sex	0800-1000	1100-1300	1400-1600	0800-1000	1100-1300	1400-1600
P. kulalensis	F	18(21*)	26(33)	16(21)	25(20)	19(17)	13(17)
	M	18(29)	12(19)	14(15)	21(15)	11(14)	14(21)
A. thalassinus	M	11(25)	18(17)	12(20)	14(13)	18(29)	13(25)
	F	11(17)	24(13)	13(17)	13(25)	21(24)	19(27)
G. verticalis	M		No record		9(15)	13(13)	11(16)
	F		No record		12(19)	11(19)	11(24)
A. longipes	M	15(10)	27(12)	15(10)	12(11)	21(21)	17(11)
	F		no record		14(11)	21(13)	17(11)

Table 23 (contd.)

A. patruelis	F	10(28)	18(25)	11(21)	8(31)	17(24)	14(27)
	M	11(21)	24(9)	16(8)	8(14)	15(19)	18(12)
P. squalus	F	10(11)	8(8)	7(5)	6(3)	12(5)	16(4)
	M	6(7)	16(6)	14(5)	21(2)	12(3)	19(4)
Odontomelus sp.	F		no record		26(13)	24(5)	28(6)
	M		no record		14(3)	13(4)	27(4)
O. senegalensis	F	15(4)	39(3)	13(5)		no record	
	M	14(3)	39(4)	23(4)		no record	
A. glaucopsis	F		no record		11(8)	14(10)	13(9)
	M		no record		7(11)	13(8)	10(7)
A. pulla	F		no record		8(28)	19(20)	15(10)
	M		no record		8(10)	16(10)	10(8)
M. fasciata	M	4(10)	20(30)	13(18)		no record	
	F	8(4)	19(5)	9(5)		no record	
A. ndoloi	F		no record		13(9)	20(6)	16(11)
	M		no record		13(11)	16(8)	10(6)

*Figures in parentheses represent the numbers of crops weighed.

6. General discussion and conclusions

6.1 Study sites

The three study sites had different amounts of rainfall during this study. Gatab on Mt. Kulal had the highest amount of rainfall. Gatab also has the highest elevation of all the three sites and it is concluded that it is the orographic rainfall coupled with occult precipitation which make this site better than Luai and Balessa Kulal. Balessa Kulal, with its low elevation and no occult precipitation, is comparatively drier than the other two sites. In fact, Balessa Kulal is typical of over 80% of the IPAL study area with respect to vegetation (Herlocker, 1979).

The dense vegetation comprising annuals and perennials at Gatab is due to the relatively higher precipitation at this site. Vegetation becomes sparser as one moves to Luai and Balessa Kulal and in all three cases most of the plants were dry during prolonged dry periods. The annuals, in particular, were short-lived and in fact even a three-week dry spell made most of the plants (grasses and herbs) show signs of withering. This means that the volcanic soils here, at Gatab particularly, do not hold water for a long time. Most of the water percolates through this volcanic soil and it is this water that may be responsible for the springs that occur at the foot of Mt. Kulal. However, the big shrubs and trees at all the study sites were always green, implying that they send their roots deeper and thus reach water.

6.2 Population studies

The result of drying up of vegetation during dry periods was the decrease in number of individuals of acridids. The breeding rate was reduced and adults of some species hid in soil cracks. There were, however, some nymphs at Gatab even during dry seasons. The occult precipitation may have been responsible for this. A similar thing was observed at Balessa Kulal and such cases were before the rains started. It is possible that the nymphs observed during the dry period at Balessa Kulal must have been surviving on dwarf shrubs. It is also concluded that the eggs may have received some moisture for development as this is essential (Joyce, 1952). One possible source of such moisture could be capillarity of underground water in the sandy areas. The nymphs were observed mostly in sandy areas of this site.

After the long rains in April the density peaks of acridids showed an elevational pattern. Thus the higher Gatab, had the peak first, followed by Luai and Balessa Kulal. The density of acridids therefore depends on vegetation quality and a change in vegetation greatly affects the density (Hemming, 1966). Vegetation quality also determines egg production as was shown during the present study.

It is mainly the protein content of fresh vegetation that determines this (Lee and Wong, 1978).

That Luai has the highest species diversity of all the three sites leads to a conclusion similar to that of Uvarov (1938b), that is, the desert of northern Kenya is not a true desert but a recently dessicated savannah and further that the acridid fauna here was received from Somaliland. This means that Luai has some savannah acridid species and also desert acridid species while Gatab has only the former and Balessa Kulal the latter. That no desert species were found at Gatab on Mt. Kulal means that these species are not adapted to and have not colonized the mountain. It is also possible that cold weather at Gatab could be acting as a barrier to these species. Examples of such species were *A. longipes*, *C. homalodemus* and *P. conica*. Further, the fact that Luai and Balessa Kulal have the highest number of oedipodines leads to the conclusion that this subfamily occurs generally in arid and semi-arid areas and is therefore geophilous. Exceptions were observed during this study occurring at Gatab on Mt. Kulal and these were *G. verticalis*, *M. fasciata*, *A. thalassinus* and *A. patruelis*.

6.3 Feeding behaviour

Mandibular adaptation to feeding is a function of aridity. The acridid species in arid sites are mostly mixed feeders while those in sites with ample rainfall, and hence vegetation, were shown by the present study to be either graminivorous or forbivorous. On the whole acridids have a higher affinity for grass eating then for forbs eating, and further it is mainly the more advanced species that are graminivorous. The conclusion is that grasses may have evolved more recently. It may also be deduced that, since grasses are generally preferred to forbs, some element that acridids require most in their diet occurs in grasses and that grasses and grasshoppers may have had a long association.

The time of the day when feeding activity is highest in acridids is not uniform but varies between sexes, species and seasons. Variation between sexes and species may be regarded as a means of avoiding competition for the available food. The variation between seasons is probably a response to rainfall. A knowledge of times of feeding is of use particularly if acridid pests have to be controlled by insecticides which have to be applied to the plants in the field. In order to avoid loss of effectiveness of such insecticides in killing the acridid pests the insecticides should be applied at appropriate times and this requires the knowledge of times when feeding activity is high.

Although acridids consumed only 2.17% of primary production in the IPAL study area as compared to 7% consumed by camels, sheep and goats (Field, 1979), they undoubtedly contribute to encroachment. Mammals, however, do more damage by trampling on the vegetation (Okelo and Simatwa, 1980).

Since acridids cause more damage when they occur in large numbers (Le Pelley, 1952), and particularly so in areas in which man has interfered by creating such things as irrigation schemes (Uvarov, 1957), the arid parts of northern Kenya are unlikely to support any successful agricultural activities in the future. Water from Lake Turkana could be desalinated and used to irrigate the land, but this would be an expensive exercise in the first place and later on changes in the environment caused by such irrigation schemes would create a suitable environment for certain acridids to breed in large numbers. Therefore it is absolutely essential to study such acridids before suitable conditions for breeding in large numbers are created. This is because some of them may become serious pests of cultivated crops. Perhaps the most reasonable thing would be to improve upon the existing pastoral-based economy of the nomads (Samburu, Boran, Rendille and Gabbra) in northern Kenya. It is suggested that irrigating selected portions in this area with water from Lake Turkana would ensure food availability for the livestock.

Acridologists would then be called upon to investigate the effects of acridids on such 'green pastures' and to establish whether the large numbers of acridids that may occur due to such changes in the environment do compete with livestock for the available food.

There is less risk in the 'green pastures' approach as compared to cultivation of crops. The reason is that 'green pastures' would comprise mainly plants such as *D. eremophilum*, *A. mutabilis* and *I. spinosa* which have had time to evolve along with the acridids and large herbivores in this area. Cultivated crops would undoubtedly be exotic to the area, particularly the lower parts, and since there will have not been time for the cultivated crops to evolve together with the acridid species of the semi-arid areas and large herbivores, an ecological equilibrium would not be guaranteed. Further it is known that acridids pose some problems in relation to the development of arid lands (Uvarov, 1956), particularly such developments involving major changes in the condition of the environment such as irrigation schemes (Uvarov, 1957).

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