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Source: Journal of East African Natural History, 87(1) : 221-232

Published By: Nature Kenya/East African Natural History Society

URL: https://doi.org/10.2982/0012-8317(1998)87[221:ACOTGF]2.0.CO;2

Journal of East African Natural History **87**: 221–232 (1998)

A COMPARISON OF THE GRASSHOPPER FAUNA (ORTHOPTERA: ACRIDOIDEA & EUMASTACOIDEA) OF THE ULUGURU MOUNTAINS AND THE EAST USAMBARA MOUNTAINS, TANZANIA

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ABSTRACT

The grasshopper fauna of the Uluguru Mountains and the East Usambara Mountains is compared. There is a marked relationship between habitat and similarity in species composition. The faunal similarity between sites rises with distance from the forest, evidently because the savannah species are widespread species that are recently colonising degraded areas, while forest faunas have a high level of endemism and flightlessness, indicating a long history of isolation and evolution. Flightlessness seems to be a result of a lower investment in wing and egg production and higher investment in prolonging life span, supported by a high persistence of the habitat and a high predation pressure.

INTRODUCTION

The Eastern Arc Mountains are known for their high levels of endemism (Rodgers & Homewood, 1982; Hamilton & Bensted-Smith, 1989; Iversen, 1991a, 1991b; Lovett & Wasser, 1993). As for other taxa, the grasshopper fauna consists of many endemic species and genera, most of which are confined to the forest (Hochkirch, 1996a). The main cause for the high degree of endemism in the Eastern Arc fauna seems to be the stable climate during periods of aridification (Scharff, 1993). The endemic taxa are considered to be a mix of palaeoendemics (relicts of a former pan-African forest) and neoendemics (recent immigrants from other habitats). In contrast to this most of the endemic species of the young volcanic mountains (Kilimanjaro and Mount Meru) are regarded as neoendemics (Wasser & Lovett, 1993).

The Eastern Arc Mountains are Precambrian basement rocks, which were faulted during the Miocene (Iversen, 1991b), while Kilimanjaro and Mount Meru are only one to two million years old (Griffiths, 1993). The time of speciation of grasshoppers within the mountains of the Eastern Arc remains unknown. However, recent mtDNA data (12S rRNA, ND1, ND5) from the genus *Parodontomelus* suggests that some of the species date back to the pre-Pleistocene, while the species of the genus *Afrophlaeoba* seem to be much younger (Hochkirch, 1999).

The Usambara Mountains and the Uluguru Mountains are probably the best-studied mountain ranges of the Eastern Arc. Many biological papers on those mountains are

available, but only few of them deal with insects and nearly none with grasshoppers. Due to the high quality of the recent taxonomic work of the Natural Resources Institute (UK), the knowledge on biodiversity of East African grasshoppers has strongly grown (*e.g.* Jago, 1996). The basis for ecological and biogeographical work on grasshoppers is now much stronger and they are suitable for research projects in East Africa.

No comparative study of the grasshopper fauna of the Eastern Arc Mountains is available. Nearly all literature on East African grasshoppers concerns taxonomy or pest control. The only ecological information on some Eastern Arc species are in the papers of Phipps (1959, 1966, 1968), who studied grasshoppers at the bottom of the East Usambaras (Muheza, Mlingano, Kibaranga) and the Uluguru Mountains (Morogoro). The first detailed ecological studies from the East Usambaras have been recently published (Hochkirch, 1995, 1996a, b, 1999).

In this paper the grasshopper species composition of different habitats in the Uluguru Mountains and the East Usambara Mountains are compared and correlated with data on the life history.

METHODS

The grasshopper fauna of the East Usambaras was studied from 11 June to 13 November 1994, from 25–29 March 1997 and from 1–24 January 1998 near Amani (all study sites presented in Hochkirch, 1996a). The grasshopper fauna of the Ulugurus was studied from 8–13 March 1997 and from 6–22 December 1997 near Morningside, above Morogoro (old road to Morningside Hotel from Morogoro up to the top). In both areas collection took place during the daytime from 10:00 to 18:00. All species of Acridoidea and Eumastacoidea sitting on herbage, shrubs and on the ground were collected. Numbers of specimens were classified into four categories for every site: Single specimen (1) = one specimen; occasionally (2) = less than ten specimens; dispersed (3) = more than ten specimens; common (4) = more than ten specimens in high densities. When nymphs were identifiable, their presence was also recorded.

The study intensity differed between the sites. The most intensely studied sites in the East Usambaras were the Mbomole Hill, a swamp near Amani, the road from Amani to Mbomole and a shortcut to Mbomole (west of the swamp). The most intensely studied sites in the Ulugurus were located along the old road to Morningside. The main part of the collection was undertaken at forest edges, or in the shade of single trees in both areas. Species within categories three and four can usually be completely recorded within a few days. Rare species, such as arboricolous forms can only be found by chance. The coverage of forest near Amani was higher than near the Morningside Hotel (only four visits inside the forest). This might result in a lower number of arboricolous species being recorded from the Uluguru Mountains.

Literature data on species not recorded during this survey has only been considered when it concerns species recorded here, or genera that were found in only one site by the author. Literature on other genera and species has not been analysed, since there is usually no information on the habitat of the species. Correlation of habitat with flight ability, food and life history of the species has been made by field observation and from literature data (Phipps, 1959, 1966, 1968; Robertson & Chapman, 1962; Hochkirch, 1995, 1996a, b). An indicator of disturbance was calculated as the percentage of savannah species within the total species number (excluding species of swamps) (after Hochkirch, 1996a).

All species were identified in the field using the following publications: Ramme, 1929; Uvarov, 1953; Descamps, 1964, 1973a, 1973b, 1977; Dirsh, 1965, 1966, 1970; Hollis, 1965, 1968, 1971, 1975; Jago, 1968, 1981, 1982, 1983, 1984, 1994a, 1994b; Kevan 1974, 1977; Johnsen & Forchhammer, 1975, Johnsen, 1982, 1983, 1984, 1986, 1987, 1990, 1991; Grunshaw, 1986, 1991, 1995; Hochkirch, 1996b.

RESULTS

Species composition

Table 1 shows the species composition of the two regions. The higher number of species in the East Usambaras (42 > 31) is probably an effect of the longer research period in this region.

Data on arboricolous species are not very reliable, since those species have been recorded usually only as one or two specimens. The taxonomy of the eumastacoid grasshoppers is also based on single specimens, with sometimes only the male or the female known. Due to the shorter sampling period in the Ulugurus it is not surprising that only three arboricolous species have been found there. *Plagiotriptus hippiscus* is the most widespread of them and can be found in Kenya, Uganda and Tanzania, where it also occurs on *Acacia* and bushes in dry woodland. *Euschmidtia sansibarica* has been recorded from both mountains. It is also known from Pangani and from Zanzibar. Arboricolous species have usually been found after rainfall under single trees, at the forest edge or in the forest. The genera *Mastarammea* and *Stenoschmidtia* have not been recorded from the Ulugurus, while other genera have species in both mountains.

Table 1. Species composition in the Uluguru Mountains and East Usambara Mountains, arranged into ecological groups. First column: Species list. Second column: Flight ability, indicated by the presence of fully developed hind wings (yes) or missing or reduced hind wings (no), a yes in brackets is given for dimorphic species. Third column: Habitat. Forth column: Occurrence in the East Usambaras (EU), categories for abundances (1 = single specimen, 2 = occasionally, 3 = dispersed, 4 = common), records from literature (D 64 = Descamps, 1964; D 77 = Descamps, 1977; G 86 = Grunshaw, 1986; J 82 = Jago, 1982; J 84 = Johnsen, 1984; R 29 = Ramme, 1929; U 53 = Uvarov, 1953). Fifth column: Occurrence in the Ulugurus (UL), categories are the same. Sixth column: Food, own observations, literature data and Nummelin (pers. comm.), the more frequently observed food is given first, ? = Food unknown, ?forbs = food presumably forbs

Species	Wings	Habitat	EU	UL	Food
Euschmidtia uvarovi Descamps, 1964	no		1		?
Euschmidtia sansibarica Karsch, 1889	no		D 64	2	?
Chromomastax cfr *rabaia* Descamps, 1964	no	arboricolous	1		?
Chromomastax spec.	no	species		1	?
Stenoschmidtia elegans (Descamps, 1967)	no	(also bushes)	2		?
Mastarammea karaseki (Ramme, 1925)	no		2		?
Plagiotriptus carli (C. Bolivar, 1914)	no		2		?
Plagiotriptus hippiscus (Gerstäcker, 1869)	no		D 77	2	*Acacia* leaves
Loveridgacris impotens (Karsch, 1888)	no	forest floor	2		?forbs
Loveridgacris ulugurensis (Rehn, 1953)	no	species		1	?forbs
Ixalidium transiens Ramme, 1929	no		3		leave litter, forbs

Species	Wings	Habitat	EU	UL	Food
Burttia sylvatica Dirsh, 1951	no			4	forbs
Aresceutica subnuda Karsch, 1896	no		4		forbs and grasses
Aresceutica morogorica Dirsh, 1953	no	Phytophilous		4	forbs and grasses
Acanthothericles rubriventris Descamps, 1977	no	species of		3	ferns
Rhainopomma usambaricum (Ramme, 1929)	no	clearings and	4		forbs and grasses
Usambilla affinis Kevan & Knipper, 1961	no	forest edges		3	forbs and grasses
Physocrobylus tessa Hochkirch, 1996	no		2		forbs
Parodontomelus arachniformis Jago, 1983	no		3		grasses
Parodontomelus stoltzei (Johnsen, 1984)	no			J 84	grasses
Parepistaurus pygmaeus (Karny, 1909)	no		4		forbs and grasses
Parepistaurus lobicercus Uvarov, 1953	no			4	forbs
Kassongia vittata Kevan & Knipper, 1961	no	Species	G 86	2	forbs
Afrophlaeoba usambarica (Ramme, 1929)	no	of open	4		grasses
Afrophlaeoba euthynota Jago, 1983	no	forest edges		4	grasses
Gymnobothroides pullus Karny, 1915	no	and	4	4	grasses
Paraspathosternum pedestris (Miller, 1929)	no	road edges	U 53	4	grasses
Phaeocatantops femoratus (Ramme, 1929)	yes		2		*Solanum*
Phaeocatantops sanguinipes (Uvarov, 1942)	yes		J 82	3	*Solanum*
Eupropacris pompalis (Karsch, 1896)	yes		3		*Solanum*
Eupropacris ornata (Karny, 1907)	yes		4		tea leaves
Eupropacris vana (Karsch, 1896)	yes	Species of	2		*Lantana camara*
Eupropacris obscura Miller, 1929	yes	insolated shrub		R 29	?
Heteracris coerulipes (Sjöstedt, 1909)	yes		4	4	forbs and ferns
Phyteumas olivaceus (Karsch, 1896)	yes		1	4	*Thevettia peruviana*
Acanthacris ruficornis (Fabricius, 1787)	yes		2	2	*Solanum,* forbs
Zonocerus elegans (Thunberg, 1815)	(yes)		4	4	Cassava, forbs
Dictyophorus griseus (Reiche & Fairm., 1850)	(yes)			1	forbs
Taphronota calliparea Schaum, 1853	yes			2	*Solanum,* forbs
Catantops melanostictus Schaum, 1853	yes		3	2	forbs
Oraistes luridus Karsch, 1896	yes		3	2	grasses
Eucoptacra gowdeyi Uvarov, 1923	yes			1	?forbs
Abisares viridipennis (Burmeister 1838)	yes		2	2	forbs
Cyrtacanthacris tatarica (Linnaeus, 1758)	yes	Woodland and	2		?forbs
Metaxymecus gracilipes (Brancsik, 1895)	yes	savannah	3		grasses
Acrida sulphuripennis (Gerstäcker, 1869)	yes	species	2	2	grasses
Afroxyrrhepes procera (Burmeister, 1838)	yes		1		grasses
Aiolopus longicornis Sjöstedt, 1909	yes		2		grasses
Odontomelus scalatus (Karsch, 1896)	yes		1		grasses
Humbe tenuicornis (Schaum, 1853)	yes		2	2	grasses
Trilophidia conturbata (Walker, 1870)	yes		4	2	grasses and forbs
Heteropternis couloniana (Saussure, 1884)	yes		4	4	grasses and forbs
Morphacris fasciata (Thunberg, 1815)	yes		3	3	grasses
Atractomorpha acutipennis (Guerin-M., 1844)	yes	Hygrophilous	4		forbs and grasses
Oxya hyla Serville, 1831	yes	species	4		grasses and forbs

Amongst the forest floor species, the genus *Loveridgacris* has a species in both mountains, while the genus *Ixalidium* is only present in the East Usambaras. However, the closely related (monotypic) genus *Burttia* occurs in the Ulugurus, with *Burttia sylvatica* being more confined to low herbage along paths than to the forest floor.
A similar situation can be found in the species of the forest herbage, where the genera *Aresceutica* and *Parodontomelus* are present in both regions, but with different species on each of the two mountain blocks. *Rhainopomma usambaricum* is one of the most common forest herbage species in the East Usambaras, while the close relative *Usambilla affinis* occurs more dispersed in the Ulugurus. The latter species has a wider distribution. It is also known from the Nguru and the Rubeho Mountains, but there it belongs to a different subspecies. Comparing the two mountain blocks, the genera *Acanthothericles* and *Burttia* are only known from the Ulugurus, while *Physocrobylus* is only known from the East Usambaras.

At the forest edge the similarity is more pronounced. *Kassongia vittata, Gymnobothroides pullus*, *Paraspathosternum pedestris* and *Phaeocatantops sanguinipes* are present in both regions, while the genera *Parepistaurus* and *Afrophlaeoba* have different species in each mountain block. *Phaeocatantops femoratus* is a coastal species, and is only known from the East Usambaras.

Among the species of tall shrubs, *Phyteumas olivaceus* and *Heteracris coerulipes* are present in both mountain regions. The genus *Eupropacris* has species at both sites. However, it is in need of taxonomic revision (Jago, 1984).

There is an obvious similarity of the species occurring in cultivated areas and road edges. Five of these species are not known from the Uluguru Mountains and three not from the East Usambaras, but they are also not common in the mountain block where they have been recorded. Some of them have only been found as single specimens. All other species are common in both regions. The savannah effect (the percentage of savannah species) in the Uluguru Mountains is higher (41.9 %) than in the East Usambaras near Amani (37.5 %). Species of swamps are only recorded from the East Usambaras because this habitat was not studied in the Ulugurus.

There is a marked relationship between habitat and similarity in species composition. The similarity rises with increasing distance from the forest (figure 1 & 2). Arboricolous species have a higher species overlap than species of the forest floor and clearings, but a smaller similarity than species of the forest edge. The high number of species only recorded from the East Usambaras is probably influenced by the longer period of investigation at this location.

The number of shared genera is higher in all habitats than the number of shared species, with the exception of the cultivated areas and road edges, where the number is exactly the same. This is because only one species is found in each of the savannah genera. The percentage of genera present in only one of the mountain blocks is highest within the forest (forest floor and forest clearings).

Correlations to wing development, food, seasonality and egg production

Wing development is clearly correlated to habitat (table 1). Forest species usually are flightless, while savannah and woodland species are fully winged. At the forest edge only one winged genus (*Phaeocatantops*) can be found, which has some endemic species in the East African rainforests, but also one widespread species (*Phaeocatantops sanguinipes*). All species of tall shrubs (which are restricted to the Eastern Arc and coastal forests as well) are fully winged and two of them were found in both areas. In cultivation, all species are fully winged and widespread.

Most of the grasshoppers feed on a variety of plants, but many of them are either

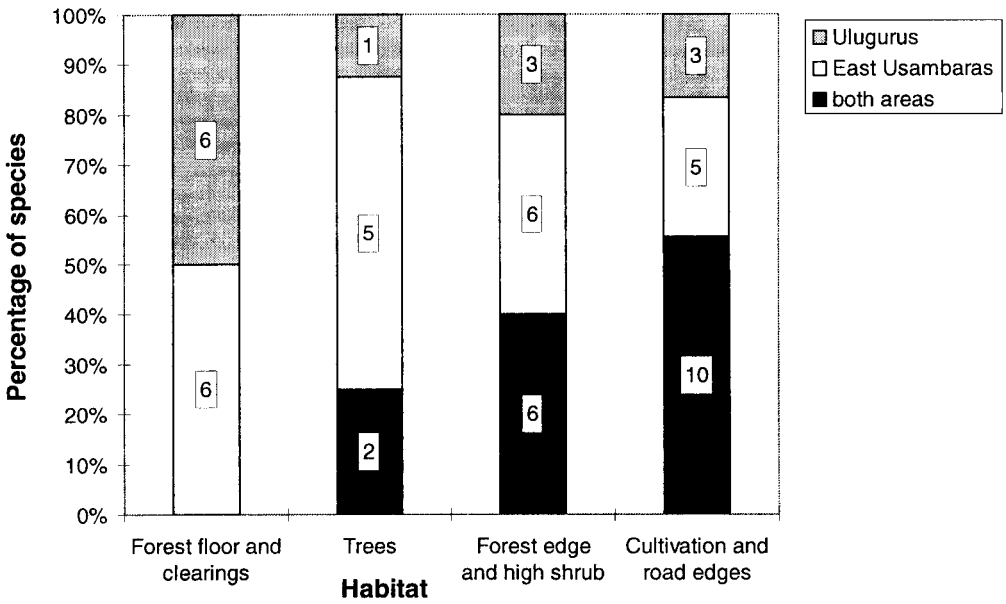

Figure 1. Taxonomic relationships between the East Usambara and the Uluguru Mountains on species level; percentage of species occurring in one (East Usambaras: white, Ulugurus: grey) or both (black) regions depending on the ecological group; numbers in the columns are absolute numbers.

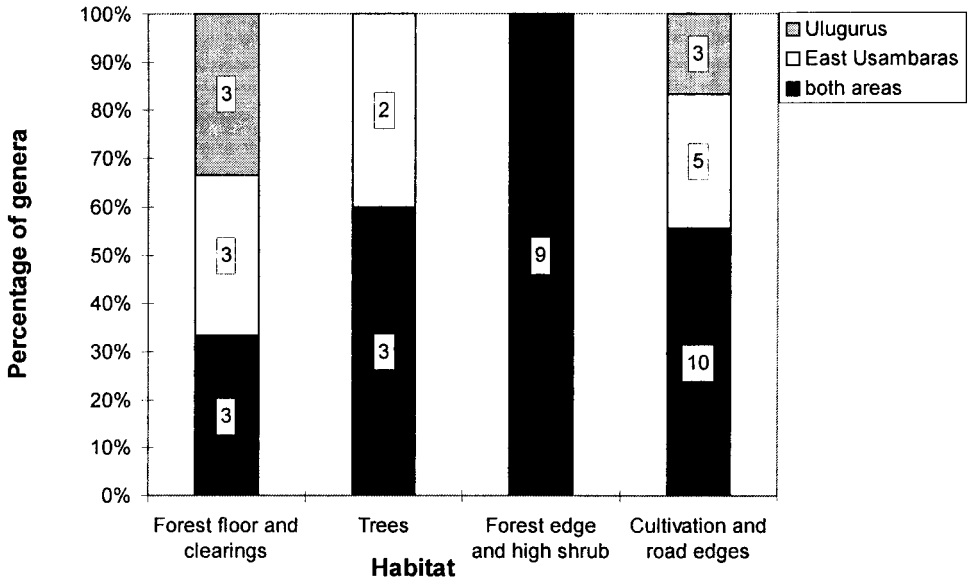

Figure 2. Taxonomic relationships between the East Usambaras and the Uluguru Mountains on genus level; percentage of genera occurring in one (East Usambaras: white, Ulugurus: grey) or both (black) regions depending on the ecological group; numbers in the columns are absolute numbers.

graminivorous or herbivorous (Hochkirch, 1996a). However, among the eight winged species of forest edges and high shrub, six (the three *Eupropacris* species, both *Phaeocatantops* species and *Phyteumas olivaceus*) were observed feeding mainly on poisonous plants, such as *Solanum robustum*, *Lantana camara* and *Thevettia peruviana*. The *Eupropacris* species and *Heteracris coerulipes* have an aposematic coloration. *Eupropacris ornata* and *Phyteumas olivaceus* are known to be rejected by birds. An *Eupropacris* species eaten by a dog almost caused its death (Jago, pers. comm.). Unfortunately data on predation pressure of grasshoppers are generally sparse and difficult to measure (Ingrisch & Köhler, 1998).

While nearly all forest species can be found throughout the year (Hochkirch, 1996a), all species of tall shrubs have a strong seasonality with adults only during the hottest season (November–March). The same is true for some of the savannah species.

There is a general trend for larger species to have a higher number of ovarioles than smaller ones (Phipps, 1959). However the number of ovarioles is smaller in the wingless forest species than in winged savannah species of comparable size (figure 3).

The correlations can be summarised as follows. In degraded areas, woodland and savannah species can be found. All of them are fully winged and have a high number of ovarioles, which means that they have bigger egg pods. The forest species are usually flightless and have smaller egg pods. A few exceptions can be found at the forest edge and in tall shrubs, where winged species occur that are also typical of the Eastern Arc. They differ from the flightless species in feeding mainly on poisonous plants, having an aposematic coloration and having a strong seasonality and a wider distribution.

DISCUSSION

A possible explanation for the high difference in species composition within the forest is the long time of separation of the Eastern Arc Mountain forests. The special location of the Eastern Arc near the Indian Ocean offered a stable climate, even in times of aridification (Lovett & Wasser, 1993). Speciation took place in isolated populations of forest taxa. In particular, populations of flightless forest species were strongly isolated from populations on other mountains, because they were not able to cross the forest gaps between the mountains. For arboricolous and forest edge species this isolation was less intense, since they were better adapted to highly insolated places, which are also more strongly affected by drought. However, mtDNA data (12s rRNA, ND1, ND5) suggests that forest edge species (*Afrophlaeoba*) were able to cross forest gaps through Riverine forests or Lowland forstes during post-Pleistocene or Pleistocene age, while forest species are much older, indicating that there was no dense forest linking the mountain blocks during the Pleistocene (Hochkirch, 1999 & in prep.). Savannah and woodland species immigrated to the mountains with deforestation. The 'savannah fauna' of the mountains is therefore much younger and more than 50 % are the same species on each mountain (figure 1). These species are also able to disperse quickly to new areas after disturbance. Wingless savannah species were not found in the area.

The higher similarity in generic composition at forest edges and on trees shows that those habitats have been less effectively isolated, or isolated for shorter periods than the forest interior, where even endemic genera can be found. On the generic level the similarity at forest edges and on trees is even higher than for savannahs. This is caused by intrageneric speciation at the forest edge and by stochastic events in the immigration of savannah species. None of the savannah genera is represented by more than one species.

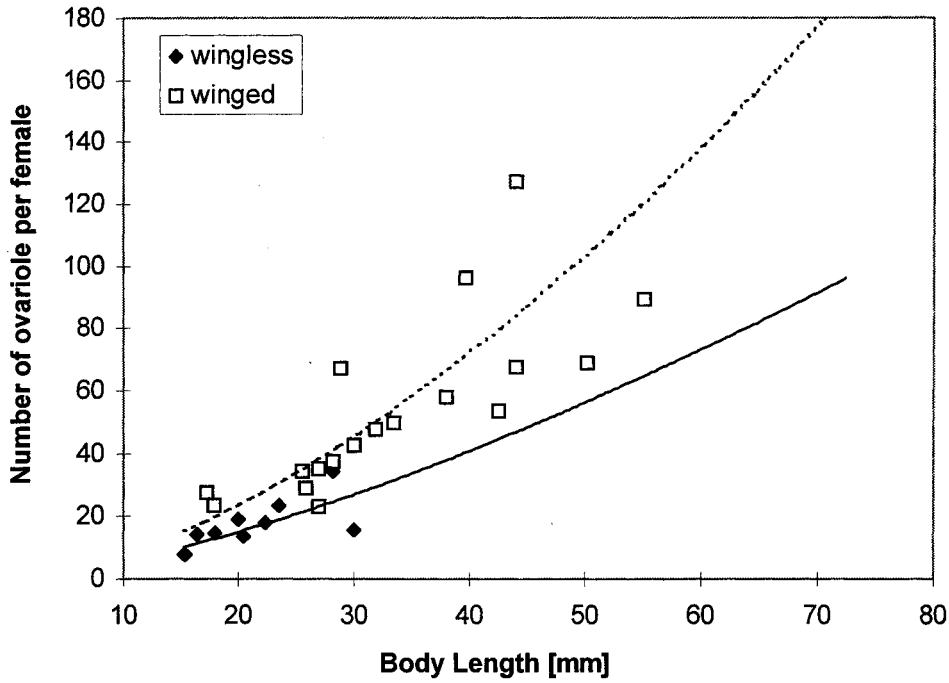

Figure 3. Number of ovarioles of winged (white) and flightless (black) grasshoppers of the East Usambara Mountains, arranged according to body length (original data from Phipps 1959).

The savannah species are good indicators of disturbance (Hochkirch, 1996a). The higher savannah influence on the Uluguru Mountains is probably caused by the large degraded areas above Morningside. The transition between open cultivation and Forest Reserve is here very abrupt. There are nearly no trees left outside the Forest Reserve. If single trees or other shaded areas occur, some forest species can usually also be found. Under big trees with a dense canopy, such as mango trees, sometimes nearly the complete association of species of forest edge, clearings and the forest floor can be found. This phenomenon can be observed at the Nguru Mountains, West Usambara Mountains and Rubeho Mountains (Hochkirch, unpubl.).

A number of factors influence the evolution of narrow range endemics (Anderson, 1994), including factors of time (climatic stability) and factors of space (refuge areas). Among grasshoppers of the Eastern Arc two factors seem to be of major importance for the evolution of species endemic to a single mountain block. The first factor is the habitat preference of the species. The number of endemics decreases with increasing distance from the forest. The similarity in species composition rises as well. This indicates that the isolation of forest species was stronger than the isolation of forest edge species. A possible explanation might be found in a better adaptation of forest edge species to events of drought, like lower water requirements during egg development, which is also known for xerophilous species in temperate regions (Ingrisch, 1983).

A second factor that supports geographic separation and small range endemism in grasshoppers is flightlessness. The evolutionary processes leading to flightlessness are still discussed (Roff, 1990). According to Jago (1985) and Roff (1990) wing reduction might

allow insects to invest more energy in increased fecundity and not expend energy in development of wings and wing muscles. However, the small number of ovarioles of wingless species indicate that they do not invest more energy in egg production, but maybe on longer survival, which means increased time for reproduction. In this case there must also be a reduced risk of predation (Krebs & Davies, 1996). This hypothesis is supported by the high age of forest grasshoppers (Hochkirch, 1996a) as well as by the low number of winged species of forest edges and tall shrubs that are poisonous. Butterfly species with small egg loads are known to have longer active lives as well (Chew & Robbins, 1984). Some of the winged species of forest edges and high shrub have also bigger ranges and a marked seasonality, but data on life history of grasshoppers from the Eastern Arc are sparse. The flightless species usually have a good camouflage or other strategies for avoiding predators, like dodging. They are mainly nocturnal and show only few activities during the daytime (Hochkirch, 1996a). According to Whitman (1988) the North-American *Taenipoda eques* is aposematic and differs also from other grasshoppers, being exceptionally large and having a different life strategy. The only winged species of South-American rainforest grasshoppers are also monophagous on *Solanum* (Riede, pers. comm.). Another fact supporting this hypothesis is that flightlessness seems to be more common in females than in males, which do not need to invest as much energy in sperm production as females need to invest in egg production (Roff, 1990). There is another factor that is of importance for wing reduction — the persistence of the habitat. According to Roff (1990) a clear correlation exists between vagility and habitat persistence. Vagility is generally important in temporary habitats, where considerable species movements are necessary. Thus wing reduction may only occur in persistent habitats, where vagility is not needed for survival. Savannah species need to reproduce and spread fast, since their habitat is affected by drought, fire, animal herds and rainy seasons. Forest species are less affected by such events.

In conclusion, habitat persistence and predation risk seem to be major factors for a number of economisation strategies, such as wing reduction, slow maturation, continuous reproduction, smaller egg pods and low abundance. There is need for more basic studies on the life history of grasshoppers, particularly on food, predation and fecundity (egg sizes, oviposition rate, number of eggs per pod, number of pods per life, duration of reproductive period, longevity, duration of development of eggs and nymphs and maturation of adults) to recognise general trends among wingless and winged species, and thus to understand an important motor of speciation in the Eastern Arc.

ACKNOWLEDGEMENTS

I wish to thank Prof. Dietrich Mossakowski, for his most generous support concerning this study and helpful comments. I also want to thank my local contact, Prof. Kim Howell for his advice. Dr Nicholas D. Jago, Dr J. Mark Ritchie and Dr Stuart Green gave me a lot of helpful information on East African grasshoppers and helped me to identify the specimens. I want to thank Judith Marshall for her hospitality at the Natural History Museum (London) and for the reprint duplicates. Thanks are due to Dr Alan Tye, Dr Matti Nummelin and Dr Stig Johansson for helpful information and hospitality and Katharina Schmich for her companionship and help during the study. Prof. Jon Fjeldså and Dr Neil Burgess made valuable comments on the manuscript. This research was sponsored by the "Stifterverband für die Deutsche Wissenschaft" and a "DAAD Doktorandenstipendium im Rahmen des gemeinsamen Hochschulsonderprogramms III von Bund und Ländern". Finally, I wish to

express my thanks to the Commission for Science and Technology (COSTECH) for giving me the research clearance for this study.

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