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ABUNDANCE DIFFERENCES OF PHYTOPHAGOUS TROPICAL INSECTS: THE CASE OF FOREST GRASSHOPPERS (ORTHOPTERA, CAELIFERA)

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Zusammenfassung. Während die große Artenvielfalt zahlreicher tropischer Insektenordnungen gut belegt ist, existieren nur wenige Untersuchungen zur Häufigkeit regenwaldbewohnender Arten, die bekanntermaßen sehr selten sind. Man beobachtet beträchtliche regionale Häufigkeitsunterschiede, die am Beispiel regenwaldbewohnender Kurzfühlerheuschrecken (Caelifera) in Tieflandregenwaldgebieten Nordwestamazoniens und Borneos vergleichend untersucht werden. Verschiedene Arten dieser weit entfernten Standorte zeigen bemerkenswerte morphologische Konvergenzen, die als Anpassungen an das Leben in den Baumkronen gedeutet werden können. Heuschrecken (Acridoidea) sind jedoch auf Borneo wesentlich seltener als in Amazonien, während Grillen und Laubheuschrecken (Ensifera) an beiden Standorten eine ähnliche Abundanz aufweisen. Als mögliche Ursachen hierfür kommen sowohl die unterschiedliche Architektur der Kronenregion als auch eine geringere Zahl geeigneter dicotyledoner Futterpflanzen auf Borneo in Betracht.

Summary. While increased species diversity of most tropical insect groups is a well-established fact, Information about their abundance is scarce and it is common knowledge that most species are extremely rare One observes considerable interregional abundance differences which were analyzed by comparing population sizes of lowland rainforest grasshoppers (Caelifera) in Northwest Amazonia and Northeast Borneo. Forest grasshoppers from both sites show remarkable convergences with respect to morphological adaptations for life in the canopy, despite considerable geographic and systematic distance. Acridid grasshoppers are much rarer in Borneo than in Northwest Amazonia, while the abundance of long-horned grasshoppers (Ensifera) is similar at both sites. It is hypothesized that different canopy architecture and a lower number of palatable dicotyledonous food plants limit grasshopper abundance on Borneo.

Key words: Amazonia, Bomeo, herbivory, abundance, nutrition ecology, Orthoptera, grasshoppers.

INTRODUCTION

It is generally accepted that there is a huge number of scientifically undescribed tropical insect species, though the dimension of our ignorance is still a matter of debate (cf. Stork 1988). Increased diversity is coupled with low abundance and patchy distribution of most insect populations in tropical rain forests (cf. Elton 1973). For example, Central Amazonia is well-known for its extremely low animal biomass due to mineral deficiency (Fittkau 1985). Scarcity and considerable regional abundance differences of butterflies and birds were already observed by Wallace (1869): "The few days I stayed here [Batachian, Molukken] produced me several new insects, but scarcely any birds. Butterflies and birds are in fact remarkably scarce in these forests. One may walk a whole day and not see more than two or three species of either. In everything but beetles these eastern islands are very deficient compared with the western (Java, Borneo, &c.) and much more so if compared with the forests of South America, where twenty or thirty species of butterflies may be caught every day, and on very good days a hundred — a number we can hardly reach here in months of unremitting search. In birds there is the same difference ... Yet, along with this poverty of individuals and of species, there are in almost every class and order some one or two species of such extreme beauty or singularity, äs to vie with, or even surpass, anything that even South America can produce." These remarks seem anecdotal, but sum-marize long years of collector's experience Even today, because of different sampling methods employed at different sites, only very few studies allow a comparison of insect abundance in different tropical regions (cf. Elton 1973). Conse-quently, the comparative study of herbivore load has been tackled from the plant side by measur-ing leaf damage (Wint 1983). This study reveals a striking similarity of leaf damage levels of around 12 % in Papua New Guinea and Panama, mainly due to phytophagous insects. However, it is evident that there should be considerable regional differences with respect to the species composition of the herbivore guild. For exam-ple, in the Neotropics leaf-cutting ants alone are the top consumers (mammals included) of phy-tomass, consuming 12—17 % of the total leaf pro-duction (Cherrett 1986).

The following reflections on factors affecting phytophagous insect populations were stimulated by the observation of noteworthy abundance differences of short-horned grasshoppers (Caelifera) at a Neotropical and a Paleotropical lowland forest. Caelifera are exclusively phytophagous throughout all larval stages, in contrast to their omnivorous or carnivorous orthopteran sister group, the Ensifera (long-horned grasshoppers: crickets and katydids). For temperate zones holds that Ensifera dominate bushy or woody areas, while principally graminivorous Caelifera dominate in grasslands or savannahs (Schmidt 1987). This is no longer true in tropical forests, where a considerable number of grasshopper species feed on both mono- and dicotyledonous plants and inhabit all strata of forest habitat (Table 1). However, tropical forest grasshoppers (TFGs) have never been an esteemed prize for collectors, and two decades ago their poor representation in museum collections and the ongoing reductions of their habitat were the main reasons for Descamps (1970) to call for an increased collecting effort. Since then, our knowledge of Neotropical TFGs, though still incomplete, improved considerably, especially after the discovery of grasshoppers from the most inaccessible forest stratum, the canopy (Roberts 1973; Descamps 1976). In contrast, the TFG fauna of the Paleotropics is still poorly known.

STUDY SITES

The following observations of grasshopper abundance were made during studies on the behavioural ecology of forest grasshoppers in Northwest Amazonia (NWA) at Ecuador (San Pablo de Kantesiya, Prov. Sucumbios, lat. 0°15'S, long. 76°27"W, 300 m altitude) and in South-East Asia (SEA) at Northeast Borneo, Malaysia (Poring, Sabah, South East slope of Mt. Kinabalu; 500 m altitude). Both study sites are characterized by tropical lowland forest (for habitat descriptions see Riede 1987 for the NWA, Stein 1978 for the North Borneo site). Conspicuous colouration together with a diurnal life style and an imaginal size of at least l cm makes TFGs comparatively easy to census by scanning the Vegetation carefully with binoculars. Canopy forms were observed from platforms or walkways and searched for at logging operations.

Field observations were complemented by a study of Bornean museum material at the collections C. Willemse (Maastricht), Sarawak Museum (Kuching) and material from a collecting expedition of F. Siegert in 1986. In addition, the profound studies of Amedegnato & Descamps (1980) on the composition of Amazonian TFG communities and results from fogging operations at Celebes (Project Wallace: Butlin & Monk 1990) and Borneo (Stork 1991) were evaluated.

NEOTROPICAL FOREST GRASS-HOPPERS

A surprising number of species and genera new to science has been discovered by collecting in freshly felled trees (cf. Descamps 1976; Riede 1990 a). This canopy grasshopper fauna is especially species-rich and abundant in West Amazonian lowland forests, but impoverishes towards

TABLE 1. Species numbers and abundance of SEA and Neotropical grasshoppers (Acridoidea): Species numbers reflect the state of knowledge from 1970. "Savannah grasshoppers" comprise subfamilies Gomphocerinae, Acridinae and Truxalinae which have not succeeded in colonizing forest habitats, in contrast to "others" which recrute forest forms, the largest subfamily being the artficial assemblage of "Catantopinae".

Abundance is given äs number of individuals per tree or number of individuals in secondary formations of 500 sqm. Data from various authors: [1] regrouped after Descamps 1970, [2] Amedegnato & Descamps 1980, [3] Stork 1991, * own observations. Further details see text.

	Neotropis	South-East Asia
number of species[1] (Acridoidea)	930	821
% savannah grasshoppers (Gomphocerinae, Acridinae)	18 %	28 %
% others (mainly "Catantopinae")	82 %	72 %
Abundance		
forest canopy	6—18 ind./tree[2]	0,6 ind./tree[3]
secondary formations (500 sqm forest gaps)		
— minimal (7-yr, *Cecropia)*	9[2] ind.	0*
— maximal (21-yr)	367[2] ind.	6[4]

the East (Amedegnato & Descamps 1982). Many species are characterized by a vivid colouration, stout body form, contrasting colouration of hind femura and prolonged hind tarsae (Fig. 1). Stridulation is absent, but functional tympana are present (Riede *et al.* 1990). Protuberant eyes and characteristic hindleg movements indicate the importance of intraspecific optical communication (Riede 1987). Besides these "dendrophilous" grasshoppers, Descamps (1976) differentiates a variety of other ecological types. A rieh fauna of "thamnorhabdophilous" species inhabits shrubs and young trees in gaps and small anthropogenic secondary formations. Many of these species are brightly coloured and brachypterous or apterous.

Amedegnato and Descamps (1980) studied composition, abundance and succession of forest grasshopper populations in primary and secondary forests and their succession in indigenous old field communities at 6 Amazonian study sites (4 in NWA, one in southern Peru and one in Guyana). Abundance of canopy species varied site-specific between 6 to 18 specimens per tree. In secondary formations, composition of species communities and abundance vary with succession. It is minimal at 7 years, during dominance of the ant-inhabited *Cecropia* tree and reaches a maximum at 21 year old formations (Table 1). At Mamepo site (NWA), abundance in 21 year formation is 36 times higher than at a parcel of the most populated primary forest (Colonia, Yubineto). An equally rieh gap fauna is known from Central America (cf. Rowell 1987; Braker 1991).

Species composition and abundance of TFG observed during my field studies on behavioural ecology in the Napo area of Amazonian Ecuador was similar to the Mamepo site studied by Amedegnato & Descamps. Between 1983 and 1989 I visited 21 logging operations (Riede 1990). Canopy grasshoppers were encountered at all sites. Twenty per cent of medium-sized trees and all of epiphyte-rich emergents harboured grasshopper populations between 10 and 120 individuals at various larval stages belonging to several species. Sedentary species like *Adrolampis colombiae* or *Trybliophorus* sp. stayed at "their" trees for several days (Riede 1987). Observations of undisturbed populations were made from simple wooden platforms at 4 sites, all of which harboured small populations of canopy grasshoppers on neighbouring trees.

Gap-inhabiting species were observed in natural and anthropogenic secondary forma-

tions. Especially in the latter certain species showed increased abundance, probably due to the increase of food plants at certain successional stages. For example, in a 3 year old field of 0.5 ha small populations of *Galidacris variabilis,* each consisting of 3 and 10 individuals of different larval stages, could be found on each of its food plant *(Potomorphe peltata* (L.); Piperaceae). Interestingly, this species accepts a much wider variety of food plants in captivity which indicates that other factors like plant architecture might affect plant preference in the wild. Several species show gregarious tendencies, from small larval hopper bands between 10 and 40 individuals (Leptysminae: *Comops* sp., *Na.dia.cris* sp.) to numerous (up to 300), dense aggregations of black larvae of *Chromacris icterus* feeding on toxic Solanaceae (cf. Pfrommer 1990). With the exception of successional stages dominated by the ant-protected *Cecropia* tree, each successional stage can be characterized by a typical community of TFGs which often exceed the abundance of primary forest species.

SOUTH-EAST ASIAN FOREST GRASSHOPPERS

Our knowledge of SEA grasshoppers is founded on the early work of Ramme (1941) and the extensive taxonomic studies of Willemse (1956, 1957). Many species descriptions are based on single specimens. Type material was examined at the collection of F. Willemse, Eygelshoven; the aspect of a considerable number of species shows remarkable morphological convergences to the "dendrophilous" amazonian forms (Fig. 1). A further convergence can be observed between the SEA genus *Pemkia* (Hemiacridinae) and Neotropical genera like *Hyleacris* (Romaleidae), which are twig-mimicking, short winged forms with excavated sterna, adapted to a cryptic life on small branches ("dendrorhabdophiles"). The extreme rarity of these forms in collections indicates that these are accidental findings of a fauna limited to the tree tops. Females might descend for oviposition which could explain the elevated percentage of females among unique type material. Systematically, most of these supposed canopy forms are subsumized under the artificial subfamily Catantopinae and urgently need to be regrouped according to modern systematic criteria (cf. Table 1). In any case, they are unrelated to the strictly Neotropical Roma-
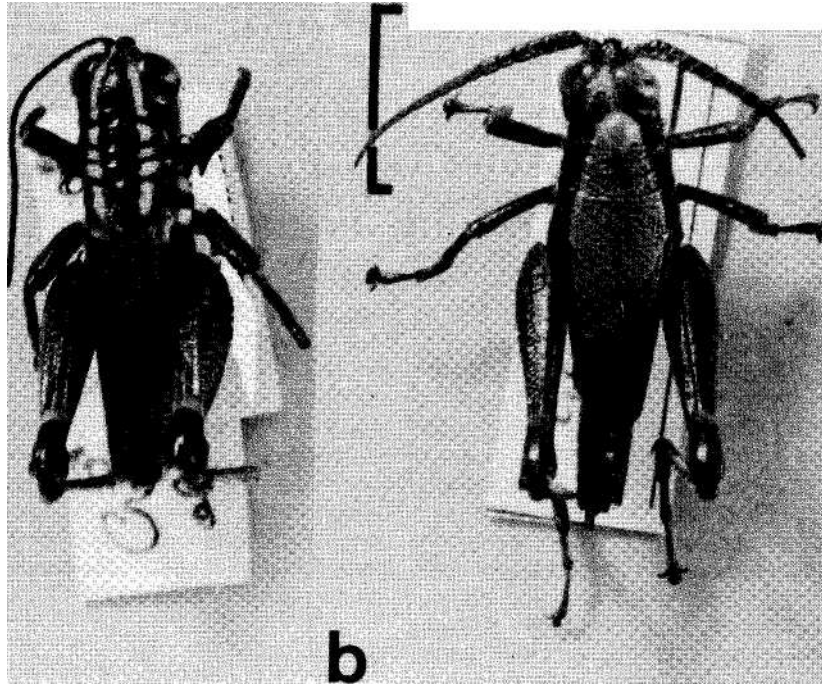
FIG. 1. Morphological convergences between canopy grasshoppers from SEA (a) and NWA (b). Both species are characterized by a vivid colouration, stout body form, protuberant eyes, contrasting colouration of hind femura and prolonged hind tarsae. a) *Craneopsis olivaceus* (Catantopinae), male, from Sibu (Sarawak), leg. F. Siegert (1986). This species was previously only known from a female specimen. The spine on the front femur is only present in the male and points to an interesting mating System, b) *Helicopacris* sp. (Bactrophorinae) from Limoncocha, Napo (Ecuador), leg. K. Riede. The red knees of hindlegs stand out from the greenish femura.

leidae, to which many canopy forms belong (cf. Amedegnato 1974). Several autochthonous genera of ancient stock are limited to Borneo and adjacent islands: the subfamily Borneacridinae is represented by the monotypic genera *Bomeacris* and *Moultonia* (Kevan 1963); the description of this subfamily was based on only 5 individuals and a single tegmen! A further example is the eumastacoid genus *Bomerianthus* (Descamps 1975).

Recent collecting expeditions to Sulawesi and Borneo did not add much to our knowledge of the supposed canopy fauna, though canopy fogging was done during both projects. Only two undescribed species were discovered besides considerable collecting effort during Project Wallace, Sulawesi (Butlin & Monk 1990). The same authors stress the low population densities of forest grasshoppers. In Borneo, Stork (1991)

found 466 Orthoptera among the 23874 arthropod specimens collected from 10 Bornean trees by insecticide fogging. The majority were Ensifera, while Caelifera were represented by only 55 individuals, with a great proportion of Tetrigidae (47), 2 Eumastacidae and only 6 acridid grasshopper specimens representing 3 species (Table 1). In a sample of similar size (24 148 specimens) from Manaus, Erwin (1983) counted 1177 Orthoptera, but did not differentiate between Caelifera and Ensifera.

At the Poring study site, a canopy walkway System of 300 m length provided access to different strata of lowland mixed dipterocarp forest at two sites 500 m apart. During a 6 weeks stay (April—May 1991), no canopy species could be spotted (2 h control walks at different times of day, every two days). During two logging operations, no canopy grasshoppers were found

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within 6 man days of intensive search. Up to now, the only canopy specimen collected during a logging Operation was found by F. Siegert at Sibu, Sarawak, in an epiphyte-rich mountain forest (Fig. l a).

In small gaps (<500 sqm) and along forest trails one regularily observes *Traulia xanthostigma.* This conspicuous species is also well represented in museum collections. It resembles the South American *Tetrataenia surinama* which inhabits forest gaps, edges and glades. Both species have light-tipped antennae which facilitate optical communication. In contrast to the gregarious South American species, populations of *T. xanthostigma* consisted of few dispersed individuals in each gap. In larger gaps (about l ha) small colonies belonging to 4 species of the genera *Meltripata* and *Systella* were observed. In one gap, a single population of 6 adult individuals of *Meltripata* sp. fed on a climber (Aristolochiaceae) and stayed on this particular plant for 10 days, though this climber was abundant all over the gap. In other gaps, this species fed on bamboo sprouts. All these gaps were inhabited by diurnal eneopterine crickets *(Nisara* sp.) in considerable densities (around 2 individuals/qm).

Dense populations of grass-feeding species like *Oxya* and *Atractomorpha* were observed in larger, anthropogenic Clearings and rice fields, but are not considered here äs they are not typical forest grasshoppers.

The extremely low abundance was confined to the Acridoidea, while other orthopteran groups were represented well. Among the Caelifera, several cryptic species of Tetrigoidea populated mossy or rotten tree trunks. *Discotettix belzebuth* inhabits humid logs were it feeds on the soft rotting wood. Fern-eating Eumastacoidea *(Mnesides* sp.) were observed regularly on their food plants along trails and in small tree-fall gaps. Among the Ensifera, a considerable number of nocturnal Tettigonioidea and Grylloidea were caught at light and monitored acoustically by sound recordings (Riede, in prep).

DISCUSSION

Summing up, it can be said that the rarity of acridoid grasshoppers in SEA is striking when compared to Neotropical habitats, while abundance of Tetrigoidea, Eumastacoidea and Ensifera does not show these remarkable differences. Our incomplete knowledge of SEA canopy grasshoppers may partly be due to their low abundance. As shown in Table l, there is a higher proportion of species belonging to grass-feeding subfamilies confined to savannah and open habitat. Bornean canopy grasshoppers do exist, but their distribution is probably so punctual that sampling efforts must be increased considerably to get series of specimens comparable to collections of Neotropical species. Such local populations are extremely susceptible to extinction, and in the light of current deforestation rates, it could be that single museum specimens will remain our only testimony of their existence. With respect to the SEA gap fauna, up to now there are no indications of such pronounced faunal succession äs known from NWA.

The data on SEA grasshopper abundance are still preliminary due to the limited number of study sites and short observation periods. There might be seasonal abundance fluctuations, including hyperannual cycles (mast years) or shifts to a nocturnal life style Despite these *caveats,* all observations indicate that forest grasshopper abundance in SEA is lower than on any known Amazonian site so that it seems justified to speculate about possible reasons. These hypotheses are by no means mutually exclusive and should also explain abundance differences within one region. They could serve äs guidelines to find those refuges where SEA forest grasshopper thrive.

Some hypotheses conceming differences in TFG abundance:

In the following, four working hypotheses on potential constraints for the abundance of TFGs are presented. The evidences are indirect and by no means conclusive. They are thought äs a framework for further investigations and more rigorous tests.

Hypothesis 1: Predation pressure Higher predation pressure by insectivore birds, mammmals, but especially ants could limit abundance of SEA grasshoppers.

Evidences:
> This is supported by a high proportion of cryptic grasshoppers (Trigonopterygidae), which in addition to crypsis exhibit a high flight distance. An adverse effect of ants on caeliferan populations is observed in SEA in the ant-rich heath forests, where Caelifera are practically absent. In successional

stages, *Macaranga* trees in SEA and *Cecropia* in the Neotropics are protected against herbivores by symbiotic ants; for *Macaranga,* Fiala (1989) has directly observed expulsion of grasshoppers by ants, for NWA, indirect evidence is provided by the low number of grasshoppers in the Cecnopza-dominated successional stage (Amedegnato & Descamps 1980).

Hypothesis 2: Canopy architecture The structure of NWA canopy is more favour-able for grasshoppers due to a more stable micro-climate and a greater number of hiding places and oviposition sites.

Evidences:

In comparison to NWA, SEA canopy is characterized by a higher number of emergents and a lower number of epiphytes (Whitmore 1984). Microclimatic fluctuation above the lower boundary of the canopy ("inversion zone": Halle *et al.* 1978) are considerable, especially at the Poring walkway site due to a rugged terrain and extremely high trees. Crown "shyness" is an additional feature supporting the more lofty aspect of Bornean forest. It gives ample room for the rieh flying fauna of otherwise earthbound animals like frogs and lizards. In comparison, NWA canopy is a monolayer of low height between 25—30 m with heavy epiphyte load and rieh humus accumulations providing shelter and Substrate for oviposition. Note that most of the SEA museum material of supposed canopy grasshoppers are females which might have descended to oviposit for want of canopy humus.

Hypothesis 3: Plant diversity Higher plant diversity in SEA hampers discovery and colonization of potential food plants by specialized herbivores of low mobility or host finding capacity.

Evidences:

Especially the Kinabalu area, is famous for its elevated floristic diversity (Stein 1978), which could exceed the host finding capacity and mobility of short-winged grasshoppers. To investigate this hypothesis, data on the degree of feeding specialization of canopy grasshoppers are necessary.

Hypothesis 4: Plant palatability Low grasshopper abundance could be a consequence of a lower number of potential food plants in SEA due to an elevated proportion of toxic plants in SEA compared with NWA.

Evidences:

Compared with temperate regions, an elevated proportion of rain forest plants contains toxic substances äs a protection against herbivores (Levin & York 1978). However, very few comparative data on secondary compounds from different rain forest regions exist, and the effect of these substances on insects is debated. A study of Waterman (1983) compares total phenolics, Condensed tannin and fibre Contents from five rain forests and reveals an increased fibre content at the SEA dipterocarp forest (Sepilok, Sabah) compared with the Neotropical study site (Costa Rica). Higher fibre content implies relative N-deficiency and would especially affect the growth of first instar grasshopper larvae (White 1984), so that low grasshopper abundance could be explained by lower nitrogen availability in Bornean plants. This Interpretation would explain the greater abundance of crickets, Tetrigoidea and Eumastacoidea: adults of the abundant gap-inhabiting cricket *Nisara* feed on plants, while their larvae could overcome the critical larval stage by omnivory and switch to foliovory later during ontogeny. Tetrigoidea and Eumastacoidea feed on "primitive" plants like mosses, ferns, algae or even dead wood and it has been hypothesized by Blackith (1987) that their strategy of transferring huge spermatophores äs nuptial gifts is an adaptation to overcome the low nutritional value of these foods. The conservancy of the association between Tetrigoidea/Eumastacoidea and lower plants indicates that host plant switch to higher plants is obstructed by their toxicity.

Monk (1987) observed occasional feeding of SEA grasshoppers on "unusual" food items such äs fungi and animal fragments. Together with the feeding on senescent leaves, these strategies could be interpreted äs adaptations to N-deficiency.

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CONCLUSIONS

The study of coevolution between insects and plants is most advanced in the highly specialized butterflies and Chrysomelidae which are examples *par excellence* of the result from the arm's race between plants and insects (cf. Farrel *et al.* 1992). Grasshoppers do not show such high degrees of specialization but nevertheless are intimately related to host plant properties which may include a variety of parameters like nutritional value, toxicity, abundance and architectural properties. They feed principally on leaves throughout their life and show no major shift in feeding strategy in the course of larval development. Endosymbionts are not known from grasshoppers which makes them especially susceptible to food plant quality. These differences to other phyllophagous insects provide an additional scenario for the analysis of insect/plant relations.

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