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NICHE BREADTH AND FEEDING IN TROPICAL GRASSHOPPERS

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Abstract—Consumption indices and apparent digestibility are measured for seven species of grasshoppers from Lamto (Ivory Coast), representative of different trophic specialization steps (Le Gall and Gillon, 1989). The consumption indices vary from 0.11 to 0.34 and the apparent digestibility from 30 to 65%. Specialists are not more efficient on their host plant than are generalists on convenient host plants, but some specialists fed on plants which are not convenient for generalists. *Anthermus granosus* and *Eucoptacra spathulacauda* feeding on *Lippia multiflora* is not convenient for a generalist like *Eucoptera anguliflava*. If feeding efficiency does not seem to be a real selective pressure, it can be an important step in specialization processes, when there is an adaptation to an unusable host plant for polyphagous species.

Differences in the constitution of plant parts eaten by the grasshopper play an important role in the digestibility. The differences in the efficiency observed between the two specialists of *Lippia* are from their differences in feeding behaviour.

Key Words: Grasshoppers, Orthoptera, Acrididae, Africa, plant-insects relationships, ecology, digestibility

Résumé—Une étude a été faite sur la consommation et la digestibilité apparente chez 7 espèces de sauterelles à Lamto (Côte d'Ivoire) représentant différents élements de spécialisation alimentaire (Le Gall et Gillon, 1989). Les indices de la digestibilité varient entre 0,11 et 0,34 tandis que les indices de la digestibilité varient entre 30 et 65%.

Autant les types dits "spécialistes" s'adaptent bien sur leur plante-hôte 1, (ou abri) autant les types dits "généralistes" s'adaptent sur des plantes-hôtes appropriées. Mais quelques types spécialistes se nourrisent sur des plantes indigestes à des types généralistes. C'est la cas de l'*Anthermus granosus* et de l'*Eucoptacra spathulacauda* qui se nourrisent sur le *Lippia-multiflora*, lequel est justement indigeste pour un type généraliste comme l'*Eucoptacra anguliflava*.

Si le comportement alimentaire ne semble pas être véritablement un critère de catégorisation, il peut toutefois jouer un rôle déterminant dans les processus de spécialisation pour ce qui est du cas des espèces polyphages devant s'adapter à une plante-hôte inhabituelle.

Les différences dans les dimensions des morceaux des types rongés par les sauterelles jouent un rôle important dans la digestibilité. La différence observée dans la capacité d'agir entre les deux types de spécialistes *Lippia* était due aux différences dans leurs habitudes alimentaires.

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INTRODUCTION

Review of literature and our results do not show a true statistical difference between graminivorous and herbivorous species. But, there is a shift from low values in graminivorous species to high values in herbivorous species. The efficiency attributed to grasshoppers (Slansky and Scriber, 1982) may be understood by the fact that only graminivorous and mixed feeders were studied and are not exact representatives of herbivorous grasshoppers, which represent half of the species in guinean savannas (Le Gall, 1986).

Diet plays a major role in the ecological niche of phytophagous insects. Plants are not only the nutrient source, but also the habitat of these insects (Strong et al., 1984). It is difficult to know the prevalence of one factor against the other. Is it the physiological or the ecological pressures that play the major role in specialization processes?

Grasshoppers show a large spectrum of trophic specialization (Uvarov, 1977; Otte and Joern, 1979; Le Gall, 1986; Le Gall and Gillon, 1989). Three different types of feeders are described, grass-feeders, mixed-feeders and forb-feeders (Isely, 1938, 1944; Gangwer, 1962; Chapman, 1964; Uvarov, 1977; and a lot of others). Grasshoppers are a good model in flood energy studies and a lot of papers give their consumption indices and their digestive efficiency (Wiegert, 1965; Gillon, 1968, 1970, 1972; Chlodny, 1963; Gyllenberg, 1970; Matsumoto, 1970, 1971). Only a few of them give the comparison of different species. Wiegert (1965) and Bailey and Mukerji (1976) compare *Melanoplus bivittatus* and *Melanoplus femurrubrum* and Chlodny (1969) compares *Chorthippus montanus* and *Chorthippus dorsatus*. These four grasshoppers have the same ecology and about the same food habits. Results given by Gillon (1968, 1969, 1972) can be used in the comparison of ecologically different grasshoppers: A polyphagous grass-feeder, *Orthochtha brachycnemis;* a stenophagous grass-feeder, *Anablepia granulata*, and a polyphagous forb-feeder, *Catantopsilus taeniolatus*.

Data on consumption and digestive efficiency of stenophagous grasshoppers is lacking. There is data on consumption and the digestive efficiency of only two stenophagous species, *Trimerotropis saxatilis* specialized on mosses and *Bootettix punctatus* specialized on *Larrea tridendata* (Mispagell, 1978). Mosses and *Larrea* are too peculiar to give a good idea of the efficiency of other specialists.

At Lamto, diets of a lot of species, grass-feeders (Hummelen and Gillon, 1968; Mestre, 1985) and forb-feeders (Le Gall , 1986; Le Gall and Gillon, 1989) are known.

MATERIALS AND METHODS

Seven species of grasshoppers have been studied (Table 1). Grasshoppers were collected near Lamto's station (Ivory Coast), the day or the week (for rare species) before the experiments which took place in September–October 1982 and April–June 1983 during the rain season. All species were in sexual activity and sometimes eggs were laid in cages.

Four vegetal species were used in these experiments:

(1) *Harungana madagascariensis*: an Hypericaceae on which lives *St. festivus*;

(2) *Lippia multiflora*: a Verbenaceae on which live two stenophagous species, *E. spathulacauda* and *A. granosus*, but poorly used by polyphagous species;

Table 1. The seven grasshoppers studied

Grasshopper species	Diet	Diet in experiments
Eyprepocnemis plorans	Mixed-feeder	*Mucuna pruriens*
Catantops sylvestris	Polyphagous forb-feeder	*Mucuna pruriens*
Heteracris guineensis	Polyphagous forb-feeder	*Hypoesthes verticillaris*
Stenocrobylus festivus	Stenophage on *H. madagascariensis*	*Harungana madagascariensis*
Anthermus granosus	Stenophage on *L. multiflora*	*Lippia multiflora*
Eucoptacra spathulacauda	Stenophage on *L. multiflora*	*Lippia multiflora*
Eucoptacra anguliflava	Polyphagous forb-feeder	*Lippia multiflora*

Table 2. Characteristics of plants used in experiments

Species	Water content (%)	D. W. S. mg/mm
Mucuna pruriens	72	0.035
Lippia multiflora	63	0.130
Harungana madagascariensis	67	0.058
Hypoesthes verticillaris	70	0.242

Table 3. Apparent Digestibility (AD) and Consumption Indices (CI) of seven West African grasshoppers

Grasshoppers	Food plants	Number	AD	CI mg/ mg
Eyprepocnemis plorans	*Mucuna pruriens*	19	0.47 (0.09)	0.23 (0.06)
Catantops sylvestris	*Mucuna pruriens*	13	0.40 (0.14)	0.11 (0.04)
		M:10		0.17 (0.02)
Heteracris guineensis	*Hypoesthes verticillaris*		0.33 (0.08)	
		F:8		0.14 (0.02)
		M:21		0.23 (0.06)
Stenocrobylus festivus	*Harungana madagascariensis*		0.54 (0.07)	
		F:17		0.32 (0.14)
Anthermus granosus	*Lippia multiflora*	29	0.36 (0.15)	0.34 (0.11)
		M:10	0.46 (0.19)	0.25 (0.15)
Eucoptacra spathulacauda	*Lippia multiflora*	F:8	0.61 (0.11)	0.31 (0.13)
Eucoptacra anguliflava	*Lippia multiflora*	20	0.14 (0.10)	0.15 (0.05)

(3) *Hypoesthes verticillaris*: an Acanthaceae which is the preferred food plant of *H. guineensis;*

(4) *Mucuna pruriens*: a Papilionaceae commonly consumed by polyphagous grasshoppers.

Leaves are cut off plants each day and chosen for their characteristics (colour, size, position on bushes and wholeness). Water contents and specific dry weight of these plants are given in Table 2.

The experiments took place in small cages. Grasshoppers collected in the field were fed 24 hr on the plant used in the experiment after 24 hr of starvation. During 10 days of the experiment, leaves were changed every day and the pieces removed by feeding grasshoppers measured on drawing paper. Grasshoppers' fresh weight was measured at the beginning and at the end of the experiment after 24 hr of starvation, when the digestive tract was empty. The surface and the dry and fresh weight of 10 leaves of the plant given to grasshoppers were measured three times along the experiments. Two indices, Consumption Index (CI) and apparent digestibility (AD) (Waldbauer, 1968) are measured:

$$CI = \frac{C}{W \times D}$$

$$AD = \frac{C - F}{C}$$

Where C = Dry weight of leaves consumed
F = Dry weight of faeces
W = Dry weight of insects
D = Duration of experiment in a day.

RESULTS

AD vary from 0.33 to 0.61 (Table 3) except in *E. anguliflava*, which has only a value of 0.14. Its variability is low in *E. plorans, H. guineensis, St. festivus, A. granosus* and *E. spathulacauda* and is high in *C. sylvestris* and *E. anguliflava*. AD is not always higher in stenophages and polyphagous species.

CI vary from 0.11 to 0.34. There are not very high values for insects, but the experimental insects were all adults. Low AD values were found in *C. sylvestris, E. anguliflava* and *H. guineensis*; in the other species AD is about the same for polyphagous or stenophagous species.

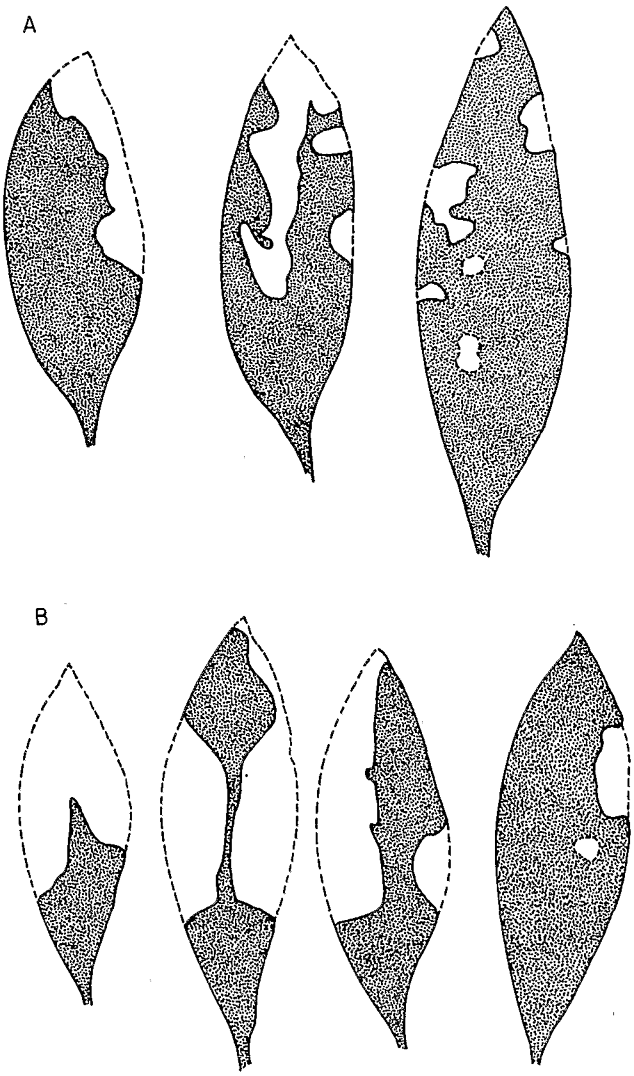

Fig. 1. Pieces of *Lippia multiflora* removed by *Eucoptacra spathulacauda* (A) and *Anthermus granosus* (B).

The shape and number of plant pieces eaten by day vary with the species of grasshopper (Fig. 1 and Table 5). The difference between *Anthermus granosus* and *Eucoptacra spathulacauda* is very significant, the former eat one big piece of *Lippia* with a large part of nervures and the latter eat several small pieces avoiding nervures. So, the AD of *E. spathulacauda* is higher than the AD of *A. granosus*.

Differences of AD between males and females are found only in *E. spathulacauda*. Differences of CI are found in *E. spathulacauda*, 0.31 in females and 0.25 in males and in *H. guineensis* 0.17 in males and 0.14 in females.

There is no compensation of low AD by high CI (Fig. 2). It is rather opposite, AD and CI being high altogether.

With our results and those from literature, (Table 4) differences between forb-feeders, grass-feeders and mixed-feeders can be found (Fig. 3). The Student's test does not show a real difference between the different types of consumers (t = 3.71, with 29 degrees of freedom for grass and forb-feeders comparison), but the figure shows a shift between values in grass-feeders and mixed-feeders and in mixed-feeders and forb-feeders, the values becoming higher when the diet comprises more forbs.

Table 4. Digestive efficiency (AD) calculated for different grasshoppers

Species	Food plants	AD (%)	References
Schistocerca gregaria	Salad	33	Chauvin (1946)
Dociaustaurus cruciger M	(2)	47.3	Nagy (1951)
Dociaustaurus cruciger M	(2)	30.2	Nagy (1951)
Oedipoda coerulescens M	(2)	20.9	Nagy (1951)
Oedipoda coerulescens F	(2)	9.5	Nagy (1951)
Orchelimum fidicinum	*Spartina alterniflora*	28	Smalley (1960)
Melanoplus femurrubrum	*Lespedza cuneata*	35.3	Wiegert (1965)
Melanoplus biliteratus	*Lespedza cuneata*	38	Wiegert (1965)
Rhabdoplea munda	Grasses	12	Gillon (1968)
Chorthippus montanus	Wheat	53.3	Chlodny (1969)
Chorthippus dorsatus	Wheat	54.7	Chlodny (1969)
Chorthippus parallelus		2 to 39	Gyllenberg (1969)
Ageniontettix deorum	*Andropogon gerardi* N	12.3	Pruess (1970)
	Andropogon gerardi K	34.8	Pruess (1970)
	Ambrosia pylostichum	0	Pruess (1970)
Ageneotettix deorum	*Andropogon gerardi* N	16	Pruess (1970)
	Andropogon gerardi K	33.6	Pruess (1970)
	Ambrosia polysticum	0 to 1.4	Pruess (1970)
Orthochtha brachycnemis	*Loudet. simplex* + *Hyp. diplandra*	8 to 13	Gillon (1970)
Parapleurus alliaceus	*Miscanthus sinensis*	20 to 23	Matsumoto (1971)
Anablepia granulata	*Brachiaria fulva*	9.6	Gillon (1972)
Encoptolophus sordidus		26	Bailey and Riegert (1972)
Oxya velox		36 to 39	Muthukrishnan and Delvi (1973)
Trimerotropis saxatilis	mushes	20	Duke and Crossley (1975)
Chrysochraon dispar M.	*Molinia coerulea*	26 to 27	Gueguen (1976)
Chrysochraon dispar F	*Molinia coerulea*	8.1 to 9.1	Gueguen (1976)
Melanoplus femurrubrum		37 to 48	Bailey and Mukerji (1976)
Melanoplus bivittatus		41 to 47	Bailey and Mukerji (1977)
Schistocerca gregaria		44 to 46	Carefoot (1977)
Paprides nitidus M		39	White (1978)
Bootettix punctatus	*Larrea tridendata*	20 to 30	Mispagell (1978)
Paprides nitidus F		30	White (1978)
Sigaus australis M		31	White (1978)
Sigaus australis F		23	White (1978)
Brachaspis nivalis M		34	White (1978)
Brachaspis nivalis F		29	White (1978)
Myrmeleotettix maculatus M	*Agrostis setacea* + *A. tenuis*	23.2	Gueguen and Delaunay (1980)
Myrmeleotettix maculatus F	*Agrostis setacea* + *A. tenuis*	31.1	Gueguen and Delaunay (1980)
Chorthippus parallelus	*Dactylis glomerata*	12	Kohler and Schaller (1981)
Machaeridia bilineata	*Loudetia simplex*	35.5 to 40	Mestre (1981)
Parahieroglyphus bilineatus M	*Desmostachya bipinnata*	44	Vats and Kaushal (1981)
Parahieroglyphus bilineatus F	*Desmostachya bipinnata*	60	

Table 5. Proportions of different types of plant pieces removed by the grasshoppers in one day

Pieces removed	*Anthermus granosus* %	*Eucoptacra spathulacauda* %	*Eucoptacra anguliflava* %
A	49	3	10
B	15	9	4
C	14	13	31
D	14	78	49
E	8	3	6

A—One big piece is eaten.
B—Different shape of pieces are eaten.
C—One little piece is eaten.
D—Several little pieces are eaten.
E—No eating.

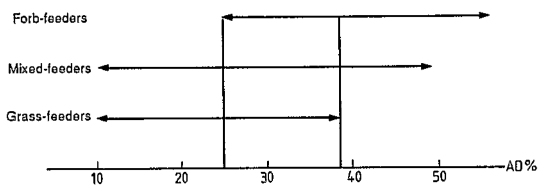

Fig. 2. Examples of plant pieces removed by grasshoppers.

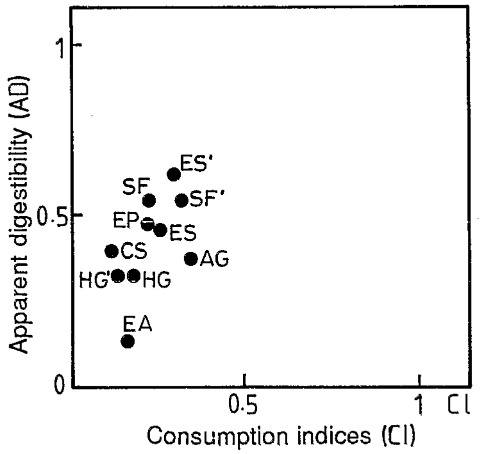

Fig. 3. Relationship between apparent digestibility (AD) and consumption indices (CI) in seven species of West African grasshoppers EP: *Eyprepocnemis plorans* fed on *Mucuna pruriens*; CS: *Catantops sylvestris* fed on *Mucuna pruriens*; HG: *Heteracris guineensis* fed on *Hypoethes verticillaris*; SF: *Stenocrobylus festivus* fed on *Harungana madagascariensis*; AG: *Anthermus granosus* fed on *Lippia multiflora*; EG: *Eucoptacra spathulacauda* fed on *Lippia multiflora*; EA: *Eucoptacra anguliflava* fed on *Lippia multiflora*.

DISCUSSION AND CONCLUSION

AD is lower in grasshoppers than in other leaf-chewing insects, like Coleoptera or Lepidoptera (Slansky and Scriber, 1982). In this paper, only adults are studied, whereas other data concern nymphs or larvae (Slansky and Scriber, 1981, 1982). Therefore AD falls when the age increases (Hussain et al., 1946; Gillon, 1972; White, 1978; Vats and Kaushal, 1981).

A stenophagous diet does not always give a high AD to grasshoppers or to other insects (Schroeder, 1976, 1977; Smiley, 1978; Scriber and Feeny, 1979). Some stenophagous species have high AD, because they consume a plant with a low quantity of indigestible parts (*St. festivus*). Futuyma and Wasserman (1981) found the same in the genus *Malacosama* in which *M. americanum* (oligophage on Rosaceae) and *M. disstria* (polyphage) have the same consumption and efficiency on *Prunus serotina*.

A. granosus and *E. spathulacauda* do not have the same AD on the same plant, *L. multiflora* and *A. granosus* have the greatest AD and eat big pieces of leaf tops with nervures which are indigestible. *E. spathulacauda* eat small pieces of leaf sides without nervures and has the highest AD. In this case, behaviour plays the major role in the values of efficiency observed. *E. anguliflava*, a polyphagous species has a very low AD on *L. multiflora*. *L. multiflora* is least consumed by grasshoppers and other leaf-chewing insects (caterpillars are very rare on this plant, pers. observ.; R. Vauttoux pers. commun.), *A. granosus* and *E. spathulacauda* got specialized on these plants, perhaps because there were no competitors.

Forb-feeders have higher AD values than mixed- or grass-feeders. This is probably the result of the grass content in indigestible molecules (silica) and the size of the plant particles ingested, grass-feeders ingesting long and large pieces of leaves less accessible to enzymes than the smaller piece of forbs ingested by forb-feeders. Adaptation to grass-feeding reduces the AD. AD has no selective value except if it is considerably reduced. When AD on a plant is too low it keeps the consumption of this plant off. Specialization does not act by increasing the AD. If there is a role of digestive efficiency in specialization process, it plays this role by permitting the consumption of unusable plants for the majority of grasshoppers or leaf-chewing insects.

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