Chapter 11

THE INVERTEBRATES OF THE GRASS LAYER

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INTRODUCTION

The most abundant invertebrates of the savanna grass layer are the arthropods. Among them, spiders and insects are most prominent, though ticks may become very numerous wherever their mammalian hosts are abundant. The status of phytophagous mites (Acari) has not yet been elucidated in tropical savannas.

Occasionally, when atmospheric moisture is high enough, land gastropods may constitute a rather important part of the invertebrate community of the grass layer. For example, the density of snails may reach seven to eight individuals per square metre on the Laguna Verde study site, Mexico (Halffter and Reyes Castillo, 1975), and up to ten individuals per square metre in some natural grasslands of Mount Nimba, Guinea (Lamotte et al., 1962).

THE DOMINANT GROUPS OF SAVANNA ARTHROPODS

The relative importance of the various taxonomic categories of arthropods is very different in open savannas and in tropical forest habitats, although comparison is made difficult by the lack of any reliable sampling method for the forest canopy. Furthermore, some arthropod groups play a major trophic role in savanna communities and are represented there by very characteristic taxa (Pollet, 1972; D. Gillon and Gillon, 1974; Lachaise, 1974).

The relative numbers and biomasses of the major arthropod groups in the grass layer of two West African study sites are represented in Fig. 11.1 (see also Tables 11.1 and 11.2 for Lamto).

Among primary consumers, the short-horned grasshoppers (Acrididae) rank first in the two areas studied; at the beginning of the dry season they represent 49.7% of the arthropod biomass at Fété Olé (Senegal), and 41.8% at Lamto (Ivory Coast). A very similar percentage (50%) has been found by Morello (1970) in periodically burnt pastures of the Argentinian chaco. Other primary consumers well represented in West African savannas are jumping plant lice (Psyllidae), white flies (Aleurodidae), plant lice (Aphididae), leafhoppers (Jassidae), and plant bugs (Coreidae, Lygaeidae and Pentatomidae) among Hemiptera, Elateridae among Coleoptera, Chloropidae among Diptera, Satyridae and Pieridae among butterflies, as well as some noctuid moths whose larvae (army worms) feed upon grass.

By far, the most numerous invertebrate secondary consumers in the two African sites studied are the spiders. At Lamto, they make up from 15 to 29% of the arthropod biomass according to the season, and 4 to 12% at Fété Olé. In both areas, four families are particularly well represented in the spider community, but in different proportions: the Thomisidae, Salticidae, Drassidae and Lycosidae (Blandin, 1974; D. Gillon and Gillon, 1974). Together with the ants (see Ch. 24), their trophic impact upon other invertebrates must be considerable. In the savannas of the Argentinian chaco, the mygale spiders are also considered by Morello (1970) as one of the most important invertebrate predators. Other predators and parasites well represented in West African savannas are the Mantodea among orthopteroid insects, the Reduviidae among Hemiptera, the Diopsidae, Chloropidae, Bombyliidae, Dolichopodidae and Tachinidae among Diptera, the Meloidae among

LAMTO   FÉTÉ_OLÉ

Spiders	Silver fishes
Grasshoppers	Tetrigids
Heteroptera	Leafhoppers
Tenebrionid beetles	Other beetles
Diptera (Brachycera)	Other arthropods
Cockroaches	Mantids
Crickets	Tettigonids
Carabid beetles	Click-beetles
Caterpillars	Hymenoptera

numbers

100 individuals per 100 sq.m.
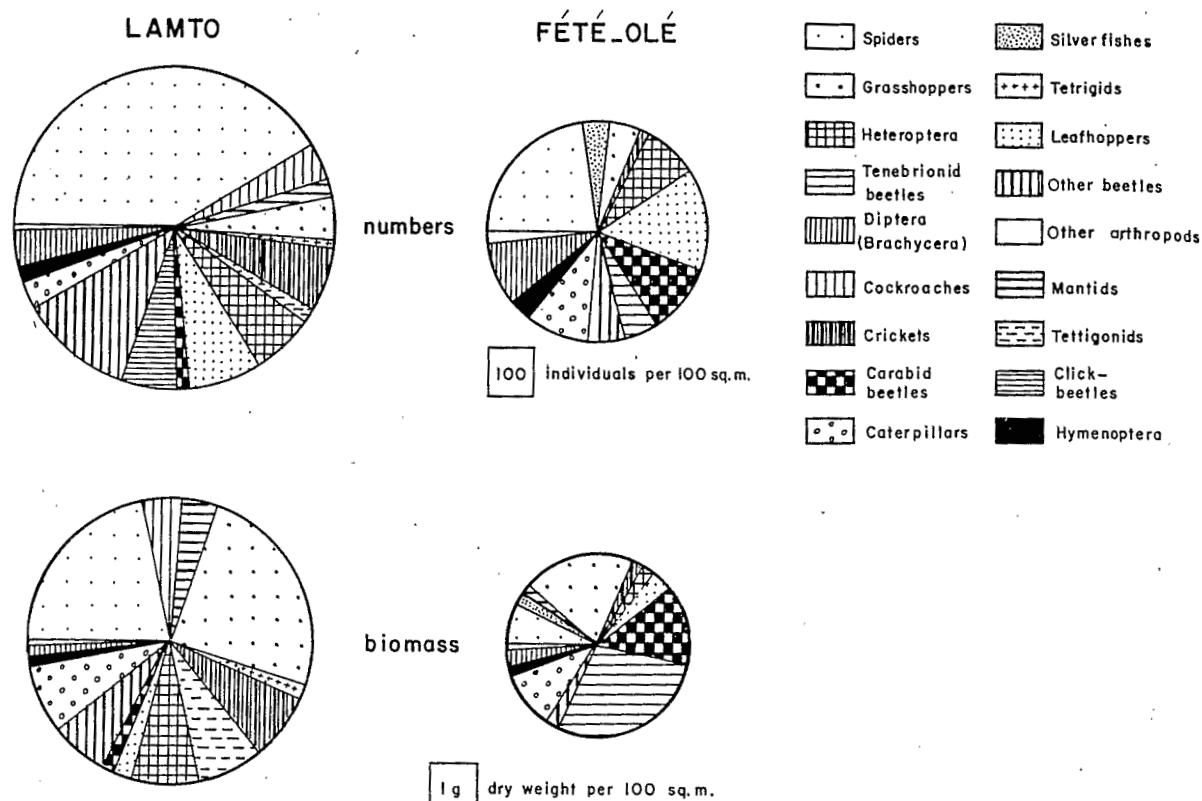
biomass

1 g dry weight per 100 sq.m.

Fig. 11.1 Numbers and biomasses of the major groups of grass layer arthropods, in two contrasted West African savannas, at two different times of the year, the rainy season (left) and the dry season (right). After Gillon and Gillon (1974).

Coleoptera, and the Sphecoidea among Hymenoptera.

Saprophages are numerous among savanna arthropods. The most common are obviously the termites (see Ch. 23), but other groups are also well represented, such as the Calliphoridae and Drosophilidae among Diptera. The silverfishes (Thysanura), cockroaches (Blattidae) and crickets (Gryllidae) are far less numerous in savannas than in forest habitats. The same is true for Diplopoda (Chilognatha and Polydesmoidea).

Despite many common characteristics, there are however some significant differences between the arthropod communities of the driest and the more humid savannas. Some of these differences are shown on Fig. 11.1 which compares the relative importance of the major taxonomic groups at different seasons at Fété Olé and Lamto. The most obvious is the predominance of tenebrionid beetles (Tenebrionidae) in the Sahelian savanna. Nineteen species have been found there, representing from 19

to 58% of the total arthropod biomass depending on the season; two species were even particularly abundant during the dry season (D. Gillon and Gillon, 1974). Other groups well represented in xeric African savannas are the Solifugae and scorpions among the Arachnida, and the Embioptera among the insects.

The seed-eating insect community is also probably different in dry and humid tropics (D. Gillon and Gillon, 1974). The few studies carried out so far on seed beetles (Bruchidae) all point out that these seed predators are extremely host-specific (Center and Johnson, 1974; Janzen, 1977).

The savanna/forest boundary sometimes has also a peculiar insect fauna. Pollet (1972), for example, has found in the Ivory Coast that Lygaeidae, Chrysomelidae, Languridae, Pipunculidae, Tenthredinidae and Chalcididae were particularly numerous at the forest/savanna ecotone. Drosophilidae are also very numerous there, more than 100 species having been collected

TABLE 11.1

Densities (ind m^{-2}) of the various groups of Arthropoda in the grass layer of the Lamto savanna (Ivory Coast) during a yearly cycle (D. Gillon and Gillon, 1974)

	Jan.	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Spiders	22.50	13.57	8.78	13.30	10.60	13.07	19.05	19.97	13.42	15.80	13.32	17.50
Opiliones							0.10	0.12	0.10	0.05	0.12	0.12
Scorpions			0.09		0.02	0.05	0.02			0.05	0.07	0.02
Blattaria	1.55	0.37	0.54	0.37	1.12	0.97	1.65	3.47	1.65	1.05	2.05	2.02
Mantodea	0.35	0.57	0.27	0.20	0.37	0.65	0.60	0.87	0.40	0.52	0.40	1.32
Acridids	0.17	1.95	2.36	2.47	1.90	2.07	1.87	1.67	1.47	1.20	0.90	1.30
Tetrigids	0.05	0.05	0.06	0.05	0.45	0.45	0.80	1.10	0.45	0.37	0.50	0.42
Tridactylids						0.05	0.12	0.25	0.87	0.15	0.05	0.10
Gryllidae	1.85	0.40	0.40	0.77	0.60	2.37	4.42	3.50	4.15	2.75	3.37	1.75
Tettigonids		0.02	0.17	0.07	0.25	0.27	0.52	0.90	1.95	1.82	1.10	0.12
Pentatomids	0.32	0.30	0.60	0.85	0.45	0.27	0.65	0.80	0.45	0.50	1.20	0.72
Coreids		0.05	0.50	0.30	0.35	0.12	0.22	0.22	0.10	0.17	0.27	0.50
Lygaeids	0.25	0.47	0.69	2.25	1.70	0.70	0.45	0.55	0.70	0.17	0.22	0.05
Reduvids	0.17	0.22	0.39	0.60	0.55	0.67	0.92	1.47	0.40	0.70	0.72	0.72
Homoptera	0.85	0.62	2.66	2.02	1.75	2.65	3.17	5.15	3.70	4.45	2.42	1.67
Carabid beetles	0.25	0.05	0.17	0.25	0.27	0.57	0.92	0.42	0.72	0.47	0.50	0.30
Tenebrionids	0.17	0.12	0.10	0.02	0.17	0.15	0.12	0.10	0.05	0.10	0.07	0.30
Langurids	0.12	0.10	0.15	0.05		0.22	0.35	0.15		0.45	0.60	0.10
Elaterids	2.12	4.07	0.45	1.45	1.50	2.75	2.20	3.40	0.95	1.20	1.82	3.37
Coleoptera (others)	0.82	0.50	1.06	1.02	18.52	2.95	2.57	2.57	4.50	7.12	3.15	2.47
Lepidoptera	1.00	1.12	1.00	1.05	0.32	0.60	0.35	0.67	0.50	2.40	1.72	1.37
Hymenoptera	0.22	0.27	0.65	0.32	0.35	0.57	0.40	0.45	0.57	0.82	0.62	0.22
Diptera	3.27	0.30	0.95	0.55	0.40	1.25	0.67	1.65	2.80	2.92	1.17	1.07
Others	0.02	0.02	0.17	0.14	0.17	0.02	0.30	0.12		1.25	0.35	0.07
Total	36.05	25.14	22.21	28.10	41.81	33.44	42.44	49.57	39.90	46.48	36.71	37.60

at Lamto by Lachaise (1974, 1979). Some species, such as *Glossina palpalis*, can also be found more abundantly at the forest edge, whereas other tse-tse flies are restricted either to savannas (*G. morsitans*) or to woodlands and gallery forests (*G. tachinoides*).

MORPHOLOGICAL CHARACTERISTICS OF SAVANNA ARTHROPODS

Size of individuals

Tropical insects are usually famous for their large size, as well as for their often unusual morphology. However, such a widely held notion needs to be supported by quantitative data. Species richness being extremely great in the tropics, and collecting being generally selective, it might well happen that large and spectacular insects are not actually more numerous here than small and dull ones, but merely

more conspicuous and hence more often collected. Unfortunately, a comparison of the size distribution of adult arthropods in various temperate and tropical communities has never been done.

However, the comparison of the live weights of all the arthropods sampled in the same way, by the same observers, on two 25-m^2 plots, in two very different West African savannas (Fété Olé and Lamto) has disclosed significant size differences between individuals in the two samples. The live weight of an average arthropod was 6.7 mg at Fété Olé, as compared with 10.2 mg at Lamto (D. Gillon and Gillon, 1974). Two explanations come to mind to account for such a size difference. First, the duration of the rainy season during which single-brooded (univoltine) species achieve their post-embryonic development is much shorter at Fété Olé than at Lamto, hence the growth period is limited. Second, the physical structure of the grass layer itself is very different in the two savannas, the grass being shorter with thinner blades in the north; a

TABLE 11.2

Biomasses (mg dry wt. m^{-2}) of the various groups of Arthropoda in the grass layer of the Lamto savanna during a yearly cycle (D. Gillon and Gillon, 1974)

	Jan.	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Spiders	100.37	45.12	42.50	76.25	39.85	59.60	59.10	79.58	39.48	72.98	84.17	78.90
Opiliones							0.47	0.40	0.61	0.37	0.60	0.60
Scorpions			1.37		0.35	0.27	0.91			0.60	1.42	0.25
Blattaria	10.25	0.62	5.22	2.37	4.58	13.17	11.01	23.25	16.36	10.15	34.83	30.50
Mantodea	3.06	5.12	18.56	8.87	6.52	15.47	10.77	9.62	3.51	41.21	4.36	13.37
Acridids	11.25	51.37	86.25	155.12	72.93	48.80	53.86	38.63	54.75	61.73	72.05	161.00
Tetrigids	0.44	0.62	0.69	0.50	5.38	7.90	7.00	15.41	4.56	3.48	4.86	4.75
Tridactylids						0.09	0.15	0.51	1.40	0.42	0.06	0.18
Gryllidae	7.12	15.75	9.47	55.00	11.38	19.16	23.87	24.71	23.48	16.41	51.73	19.69
Tettigonids		1.25	10.56	2.81	9.71	13.08	5.96	2.76	9.72	80.35	129.36	2.77
Pentatomids	2.87	4.56	6.75	11.68	9.02	5.71	19.98	17.85	8.33	6.43	20.07	9.12
Coreids		0.87	5.25	5.62	3.07	2.10	2.70	1.80	0.38	1.30	2.51	3.87
Lygaeids	0.62	1.31	1.06	5.75	3.70	1.26	1.10	2.32	0.90	0.50	0.51	0.50
Reduvids	1.87	3.00	3.39	9.50	2.62	9.78	8.40	11.66	4.32	8.77	24.06	5.62
Homoptera	0.75	2.00	6.34	7.00	3.38	8.40	9.02	10.46	5.28	10.50	9.81	6.25
Carabid beetles	2.00	0.25	3.81	8.87	5.76	7.58	12.43	4.63	15.86	15.43	11.18	5.65
Coleoptera (others)	6.00	6.75	9.06	8.65	48.32	15.20	18.28	12.58	16.30	25.80	15.15	16.87
Lepidoptera	29.31	14.81	24.47	16.90	2.50	8.57	21.92	16.07	4.63	32.73	95.13	19.87
Hymenoptera	1.50	1.37	4.65	3.12	2.22	1.62	1.02	1.23	0.73	4.66	3.85	0.87
Diptera	7.62	0.87	3.19	1.62	1.75	3.70	1.86	2.68	6.36	7.77	5.37	4.31
Others	0.12	1.25	0.68	0.93	2.01	0.21	1.01	1.46		2.00	0.85	
Total	185.15	156.89	243.27	380.56	235.05	241.67	270.82	277.61	216.96	403.59	571.93	384.94

large size would not therefore be adaptive for most arthropods of the grass layer in the Sahel. Obviously, these two explanations are not mutually exclusive.

It has also been noticed by Lachaise (1974) that the adults of related species in two families of Diptera (Anthomiidae and Calliphoridae) were smaller in savannas than in rain forests, the latitude being the same for both study sites.

Within a given taxonomic group, the average individual weight varies during the annual cycle, according to the phenology and voltinism (number of generations per year) of the species concerned. It can remain the same throughout the year, as in the case of spiders (Fig. 11.2), or can display minimum values during the rains as is the case for crickets or acridids. The seasonal variations of the average body weight of the arthropod community as a whole are rather small; they depend essentially on the weight of the univoltine species, whose individual weight is generally high and whose seasonal changes in abundance are clear-cut.

The lightest individual body weights were observed in our studies at the end of the rainy season:

5.3 mg in September in northern Senegal and 5.4 mg in September in the southern Ivory Coast (D. Gillon and Gillon, 1974). Average body weights are rather meaningless at the beginning of the rainy season, when most arthropods hatch and a large percentage of immature stages is found in any population.

External morphology

The colour and external appearance of arthropods are deeply influenced by the habitat of their adult stages and their feeding habits. Any elongated, green or straw-coloured acridid has a good chance of belonging to the grass layer community, although most arthropods living in the grass layer are not grass-mimics. Heteroptera, for instance, never mimic grass blades. The best grass-mimics are found among the larger species, such as phasmids of the genus *Gratidia*, which are even more thread-like than most other stick insects. On the other hand, the smallest insect species, such as jassids, tend to resemble seeds rather than grass.
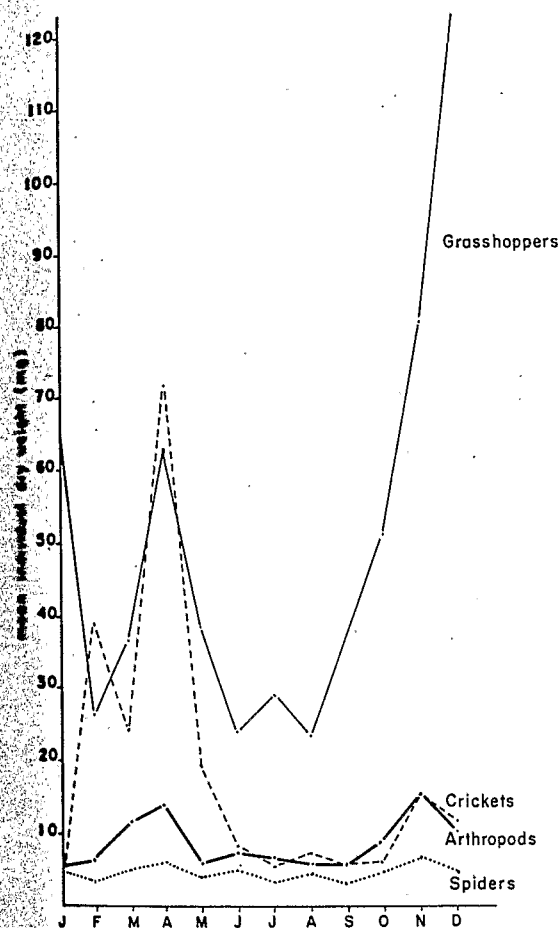
The adaptive function of the cryptic elongated

Fig. 11.2. Monthly variations of the average dry body weight of spiders, crickets and acridids, compared to that of the average body weight of all sympatric arthropods of the grass layer, in the Guinean savanna of Lamto, Ivory Coast.

body form of savanna acridids is enhanced by special concealing attitudes. The very mobile species which settle on the grass (such as members of the genera *Acrida*, *Chromotruxalis* and *Truxalis* in West Africa) have an elongated body and long, thin hindlegs which are kept well away from the body axis (Fig. 11.3). On the other hand, the more sedentary species which spend a long time on the same grass support (such as *Cannula*, *Leptacris* and *Mesopsis*) have shorter and stronger hindlegs, kept close to their body when at rest (Fig. 11.4). Among African acridids, all species with elongated bodies are graminivorous, whereas forbivorous species never display such a body-build; the same situation occurs in the llanos of Venezuela, and apparently in other tropical grasslands as well.

Similar concealing habits are also found among savanna mantids. In Africa, those belonging to genus *Pyrgomantis* (Fig. 11.5) resemble *Cannula*, whereas *Leptocola* are more similar to phasmids. Even the egg-case (ootheca) of *Pyrgomantis pallida* is elongated and cryptically coloured; the female crouches on the ootheca which is fixed on a grass blade during the entire "incubation" period. Both the adult and the egg-case are straw-coloured, and have the same elongated appearance and a similar size (Fig. 11.4). When praying-mantis species are grass- or stick-mimics, with elongated forelegs, their defensive posture is quite different from the usual "frightening" behaviour of Mantinae; they promptly protract their forelegs so that their resemblance to a grass blade or a stick is intensified (Edmunds, 1972, 1976).

Plant mimicry can also be enhanced by an increased pilosity of the cuticle in some savanna insects. A good example is *Bocagella acutipennis hirsuta*, an acridid living on the composite *Vernonia guineensis*, a common forb in the Guinean savanna of Ivory Coast. The numerous hairs on its thorax and legs, together with its very slow movements, make it almost unnoticeable on the flower head of the plant. Another example is *Anablepia granulata* which feeds exclusively on *Brachiaria* grasses.

Among heterometabolous insects, selective pressures are not only exerted upon adults but also, and probably to a much greater extent, upon the smaller juvenile stages. It is worth noting, in this connexion, that grass- and twig-mimicry are much scarcer among holometabolous insects. In African savannas at least, twig- and leaf-mimicry is found among Lepidoptera but their caterpillars generally feed more upon woody plants than on grass.

Batesian mimicry is also common in savanna butterflies, the model in this case being unpalatable sympatric butterflies. The most extensively studied example is indeed that of the African swallowtail, *Papilio dardanus*, whose females are highly polymorphic. Thirty-one different morphs have been identified so far (Clarke and Sheppard, 1960; Ford, 1971; Owen, 1971; Edmunds, 1974). Throughout much of tropical Africa the females of *Papilio dardanus* are excellent mimics of various species of Danaidae, and to a lesser extent of *Bematistes* spp. (Acraeidae). Where the models or potential models are abundant, as in lowland forest areas, most females of *Papilio dardanus* are good mimics, but
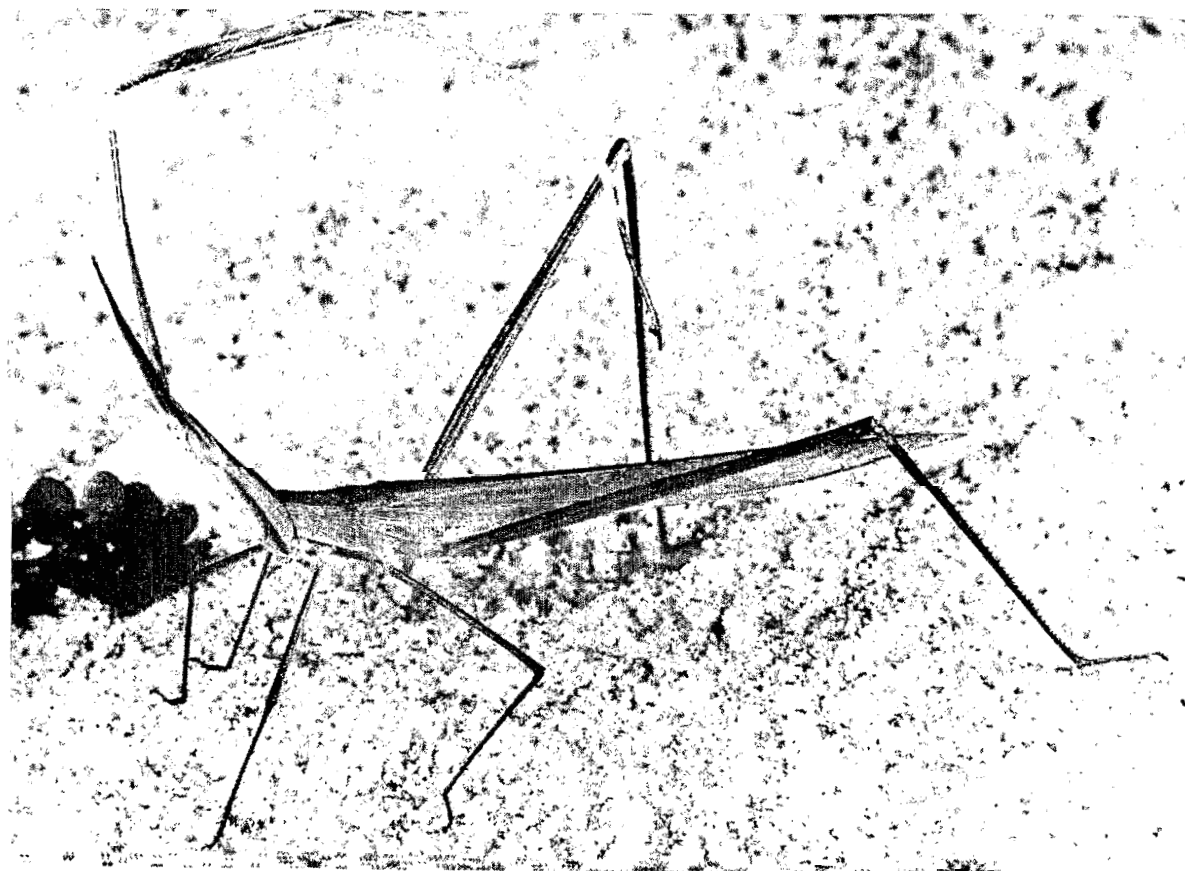
Fig. 11.3 *Chromothruxallis libenta*, a cryptic acridid of the Lamto savanna, Ivory Coast. (Photo by Y. Gillon).

where the models are rare, as in some dry savannas, non-mimetic and highly variable female forms occur (Ford, 1971).

Ant-mimicry is also common in tropical savannas. In West Africa, young stages of a number of tettigonids (*Eurycorypha*), mantids (*Gonypetella*), coreids [*Euthetus leucostictus, Mirperus jaculus* (Fig. 11.6) and *Riptortus dentipes*], and mirids (*Diocoris agelastus, Formicopsella* spp., *Leaina belua, Myombea bathycephala* and *Systellonotidea triangulifer*), very closely resemble ants, at least for a time. The well known spiders belonging to the genus *Myrmarachne* remain perfect ant-mimics throughout their life-span (Fig. 11.7). In Ghana, each species of *Myrmarachne* is positively associated with a different species of ant, and there is mutual exclusion between the three species of dominant ants. Furthermore, the early instars of *Myrmarachne* mimic different, smaller, species of ants from the adults (Edmunds, 1978). The larvae

of some assassin bugs of the subfamily Piratinae, camouflage themselves by carrying the bodies of the ants they have killed on their backs.

Concealing coloration and mimicry are scarce among ground-living savanna arthropods. Among crickets, only the bodies of those belonging to genus *Eucyrtus* are somewhat elongated. Some insects however may camouflage themselves by using sand grains: such is the case in Africa for the tetrigid *Pantelia horrenda*, the tenebrionid beetle *Vietta senegalensis* and the pentatomid *Thoria gillonae*.

Colour change to match a particular background

A cryptic animal cannot properly harmonize with its surroundings without an adequate overall colour resemblance to its background: hence, the predominance of greens and browns among the colours of insects living in the savanna grass layer.
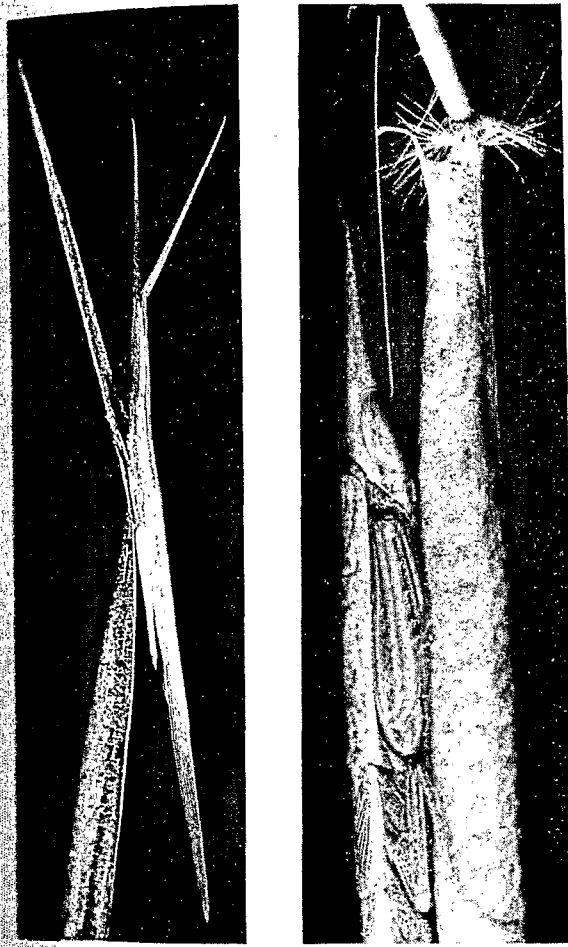
Fig. 11.4. *Cannula gracilis*, another cryptic acridid of the Lamto savanna (Ivory Coast), generally found closely applied against grass blades. (Photo by Y. Gillon.)

Fig. 11.5. Resting attitude of a female *Pyrgomantis pallida* on its ootheca fixed upon a stem of *Loudetia simplex*. (Photo by Y. Gillon.)

Some tettigonids do bear some purple body markings, but these purple marks also bear a striking resemblance to the purple areas of anthocyanin pigment that occur on very young, or very old, leaves in the habitats in which these grasshoppers live.

The tettigonid *Homorocoryphus nitidulus*, for example, has six distinct colour forms in Uganda: green, brown, green with purple stripes, brown with purple stripes, green with a purple head, and brown with a purple head. The frequency of the six forms in a large random sample from the derived savanna around Kampala (Owen, 1976) is shown in Table 11.3. Green was about twice as frequent as brown, and together these two forms accounted for nearly 97% of the sample. In the habitat studied, green was the predominant colour, brown came next, and purple (on green or brown leaves) was the rarest. Hence the three conspicuous colours in the habitat of this grasshopper were also the same colours that occurred in the grasshopper themselves. The percentages would probably be different in populations living in other savanna areas, and possibly at different times of the year. A wholly purple form has indeed been found in the small patches of savanna enclosed within the lowland rain forest of the lower Ivory Coast (Bellier et al., 1969).

The overall colour of the savanna grass layer also drastically changes with the seasons, and species have to adapt their colour so that they can harmonize with two or even three different backgrounds. This is achieved through environmentally induced polymorphism (Edmunds, 1974), a phenomenon quite common among orthopteroid insects living in the grass layer. Indeed, when two generations follow one another during the same year, the green form predominates during the rainy season and the brown form during the dry season. If a polyvoltine savanna species is monomorphic, then it is generally straw-coloured.

In the acridid *Acrida turrita*, Ergene (1950) found that green larvae placed on a yellow background changed to yellow at the next moult. However, the quality of light reflected from the background is but one of the factors determining whether a grasshopper changes colour or not. Dryness has been shown to induce a green coloration in *Acrida bicolor* and *Schistocerca vaga* (Okay, 1956; Rowell and Cannis, 1971), and Owen (1976) has noted that in *Homorocoryphus nitidulus* there was a statistical association of green with females and brown with males.

Ground-living insects are very seldom green-coloured, regardless of the number of generations per year.

After grass fires, most savanna insects, the acridids particularly, turn partially or totally black (Burtt, 1951). A wholly black female mantid *Danuria buccholzi* has even been found at Lamto, at the very beginning of the dry season, before the outbreak of the grass fires; being wingless, this mantid could not have come from very far away.
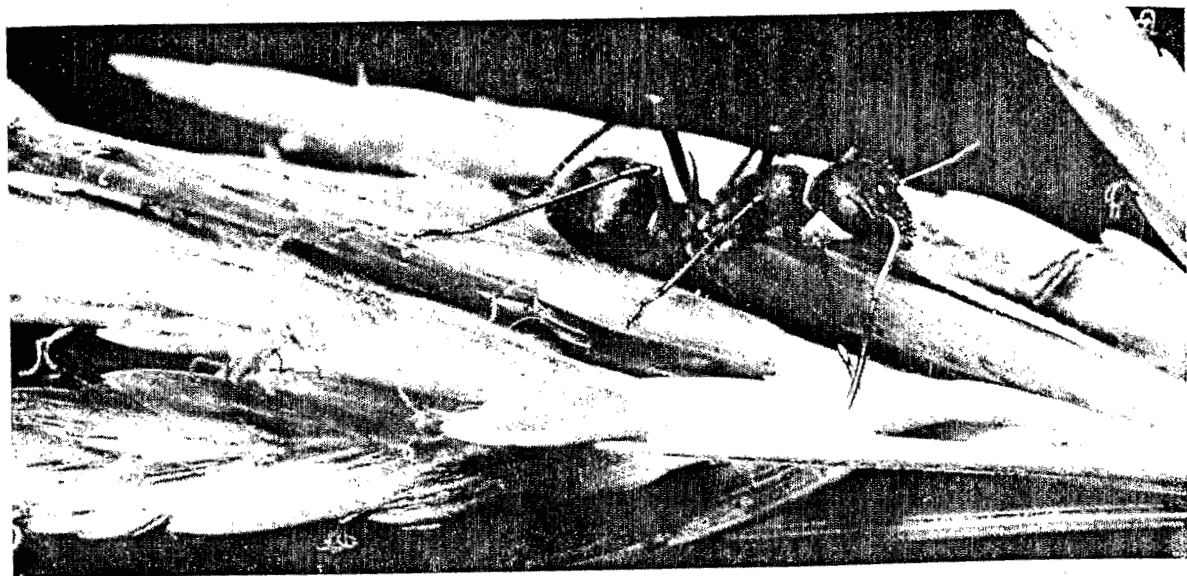
Although young and adult acridids turn black

Fig. 11.6. An ant-mimic, the young of the coreid bug *Mirperus jaculus*, on *Cyperus zollingeri*, a savanna sedge, Lamto, Ivory Coast. (Photo by Y. Gillon.)

very quickly — in less than two days during the dry season — they take a much longer time to revert to their original colour (Y. Gillon, 1971). It would be interesting to know whether the same ability exists in species whose young are found only during the rainy season. If not, this would tend to demonstrate that the selection pressure exerted by grass fires has indeed a very long history.

Whereas the gregarious phase individuals of the migratory locusts are not cryptically coloured, the solitary phase individuals keep the same cryptic colours and patterns as the solitary locust species.

Except for some beetles (Chrysomelidae. Meloidae), very few savanna insects display warning colorations. Those which do so, such as some pyrgomorphids (*Phymateus* spp., *Zonocerus* spp.) and *Staurocleis magnifica* when adult, feed exclusively on forbs.
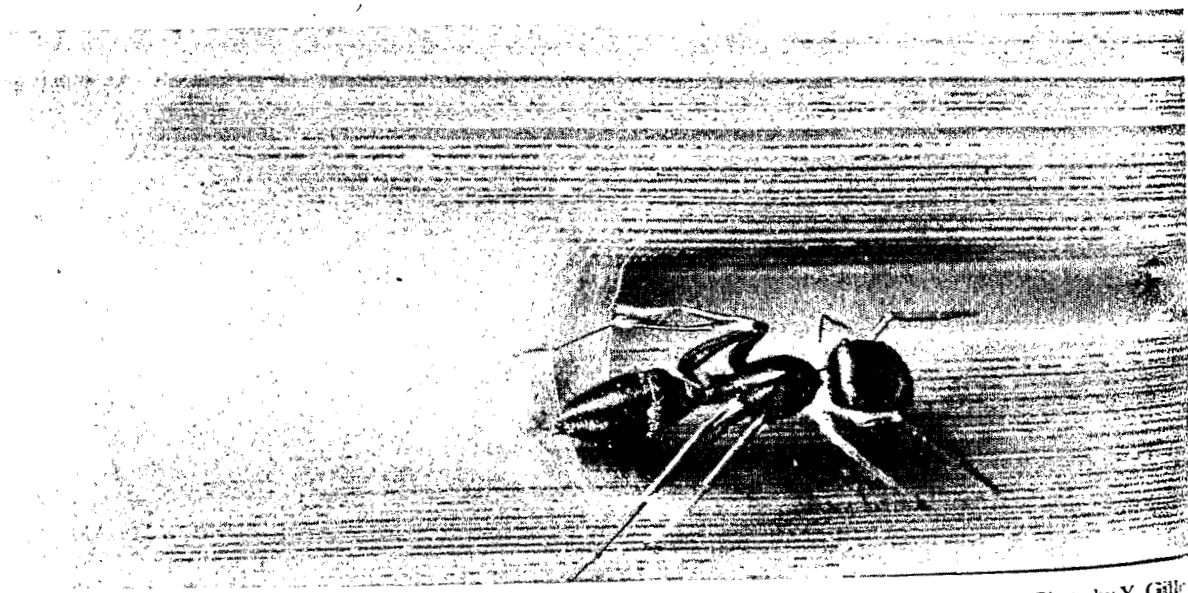
Fig. 11.7. Another ant-mimic, the spider *Myrmarachne* sp. on a blade of *Imperata cylindrica*, Lamto, Ivory Coast. (Photo by Y. Gillon.)

TABLE 11.3

Relative frequency of colour forms of *Homorocoryphus nitidulus* at Kampala, Uganda (after Owen, 1976)

Colour form	Number examined	Percentage
Green	6682	63.34
Brown	3521	33.38
Green with purple stripes	305	2.89
Green with purple head	34	0.32
Brown with purple head	5	0.05
Brown with purple stripes	2	0.02

The brightly coloured yellow or red hind-wings of some savanna acridids (*Chromotruxalis liberta*, *Gastrimagus africanus*, *Ornithacris* spp.) are always concealed when at rest. The overall coloration of those species of crickets (such as *Xenogryllus eneopteroides*) which climb grass stems and blades is more brownish than those which remain at ground level which are darker.

ADAPTATIONS TO THE SEASONAL WATER SHORTAGE

Most of the savanna insects, especially those inhabiting the more xeric grasslands, are well adapted to the seasonal water shortage — by means of a diapause during which development is arrested. Diapause can occur at various stages of the life history of a species — the egg, the pupa, or even the adult before the breeding season; more rarely at the immature stages. However, some mosquito larvae can stand prolonged dehydratation, and larvae of the chironomid *Polypedilum vanderplanki* can survive ten years of cryptobiosis (Hinton, 1960).

Most of these resistant stages survive the seasonal drought underground. Soil is loose enough during the rains to let most insects dig into it, and it becomes hard enough during the dry season to protect them from many predators. It also affords shelter against overheating during grass fires, as shown in Chapter 30. The humidity of the habitat, which in turn depends on the characteristics of the soil, has been shown to be one of the major environmental factors influencing the distribution of tropical acridids (Duranton and Lecoq, 1980). Another way for many insects to escape the seasonal drought is to move temporarily to habitats where living conditions are less severe, especially along the forest/savanna boundary. In the derived savanna in the Ivory Coast, for example, plataspidids and langurids undertake massive seasonal movements, whereas acridids, pentatomids and membracids are far less mobile, and carabid beetles and whiteflies (Aleurodidae) do not move at all (Pollet, 1972).

SEASONAL VARIATIONS IN ABUNDANCE

It is difficult to appreciate globally and accurately the seasonal changes in the numbers of an invertebrate community, even in the savanna grass layer, since the reliability of the available collecting techniques differ greatly from one taxonomic category to another. It is, therefore, only possible to compare population densities within one category of organisms (or possibly categories of closely related organisms) at different times of the year. Even in this case, it must be kept in mind that the various developmental stages of many invertebrates cannot be properly sampled quantitatively by the same technique used for the adults. Hence, a fair knowledge of the phenological cycle of at least the most abundant species present within the community is necessary.

Overall variations of the invertebrate community

Some sampling techniques are, however, more reliable than others for quantitative inter-seasonal comparisons. Such is the case for methods involving the careful hand collection of all the arthropods present in a study plot of fixed size, enclosed whenever possible in a mobile cage (a "biocoenometer", Y. Gillon and Gillon, 1965). In three African grasslands, such a method has shown that the invertebrate fauna of the grass layer is definitely more abundant during the rainy season than during the dry one.

In the derived savanna of Lamto, Ivory Coast, the overall arthropod biomass increases with the standing crop of grass (Y. Gillon and Gillon, 1967). However, whereas the average grass biomass reaches 1 kg m^{-2} (fresh weight) for at least six months during the year, that of the arthropods of the grass layer seldom attains 1 g m^{-2}. The lower biomass values are found during the dry season, in January and February, whereas peak values are

reached in October and November, at the end of the long rains (Tables 11.1 and 11.2).

However, the changes in population density do not follow the same pattern in all taxonomic categories. Four different patterns can be distinguished: (1) an increase in abundance ending with a peak during the rainy season itself; (2) an increase in abundance ending with a peak at the very beginning of the next dry season; (3) an increase continuing until the start of the annual grass fires; and (4) a multimodal pattern, with two or more peaks in numbers, or even no definite change in abundance at all.

Most insects of the grass layer follow the first pattern: cockroaches, acridids, tetrigids, lygeids, reduvids, and adult carabid beetles living above ground level [those living in the upper parts of the soil are more abundant during the dry season, according to Lecordier and Girard (1973)]. The long-horned grasshoppers (Tettigonidae) and the caterpillars of moths and butterflies follow the second pattern, whereas the Homoptera (mostly represented by jassids) follow the third one. Mantids have two peaks of abundance, as well as rutelid beetles (Girard and Lecordier, 1979). Variations in the abundance of spiders do not conform to any regular pattern.

It is worth remembering at this stage that an increase in arthropod numbers does not necessarily imply an increase in biomass, because the older the individuals become the less numerous they are. However, within a given species, the increase in body weight is generally more rapid than the decrease in numbers (Y. Gillon, 1973). Furthermore, since the larger arthropod species have a single breeding season per year, it follows that the overall maximum arthropod biomass is reached at the end of the rainy season, and not earlier. It is at that time of the year that the amount of available food is the greatest, at least for secondary consumers. The situation is somewhat different for primary consumers, because the increase in grass biomass does not go hand in hand with its nutritional value. Quite on the contrary, it is at the beginning of the rains, when fresh grass appears, that its nutrient content is the highest — precisely at the time when most acridids hatch from the egg.

Most seasonal variations in numbers or biomass imply changes in the demographic structure of the populations concerned. Every season can thus be characterized by the predominance of a particular age class among univoltine species.

In the drier Sahelian savanna of Fété Olé, northern Senegal, the overall arthropod community is four times more numerous during the short rainy season than during the long dry season (Fig. 11.8), although certain species can be more abundant during the drier part of the year (Y. Gillon and Gillon, 1973). The arthropod community of the mountain grasslands of Mount Nimba, Guinea, is also more numerous during the wettest part of the year, although large orthopteroid insects are more conspicuous during the dry season (Lamotte, 1947). Though using a much cruder technique of sampling, Dingle and Khamale (1972) also found an increased insect biomass during the long rains in the *Themeda triandra* savanna of the Athi Plains, Kenya (Table 11.4).

Seasonal variations in numbers of univoltine species

The development of arthropods, which breed only once a year, is either spread over many months, or is interrupted by a long quiescent phase during the dry season.

Such species do not maximize their natality. Their intrinsic rate of increase r is indeed influenced more by the time necessary to reach their reproductive phase than by the rate at which females produce off-spring (Lewontin, 1965). This limitation of natality is balanced by a better adaptation of each phase of the life-cycle to the prevailing environmental conditions. This does not imply that all univoltine species become adult at the same time of the year, as a number of different strategies can be adopted by sympatric species.

For example, among the nineteen species of thomisid spiders whose life-cycle has been studied by Blandin (1972) in the Guinean savanna of Lamto, Ivory Coast, eleven were univoltine. Among them, three different phenologic cycles can be distinguished: (1) in some of them, males become adult earlier than females (protandry), and females outlive males; (2) in other species, adults of both sexes disappear during the dry season, from December to February; and (3) in still other species, some breed at the beginning of the rains, from April to June (*Runcinia sjoestedti*, *Stiphropus niger* and *Thomisops lesserti*, for instance), whereas others d

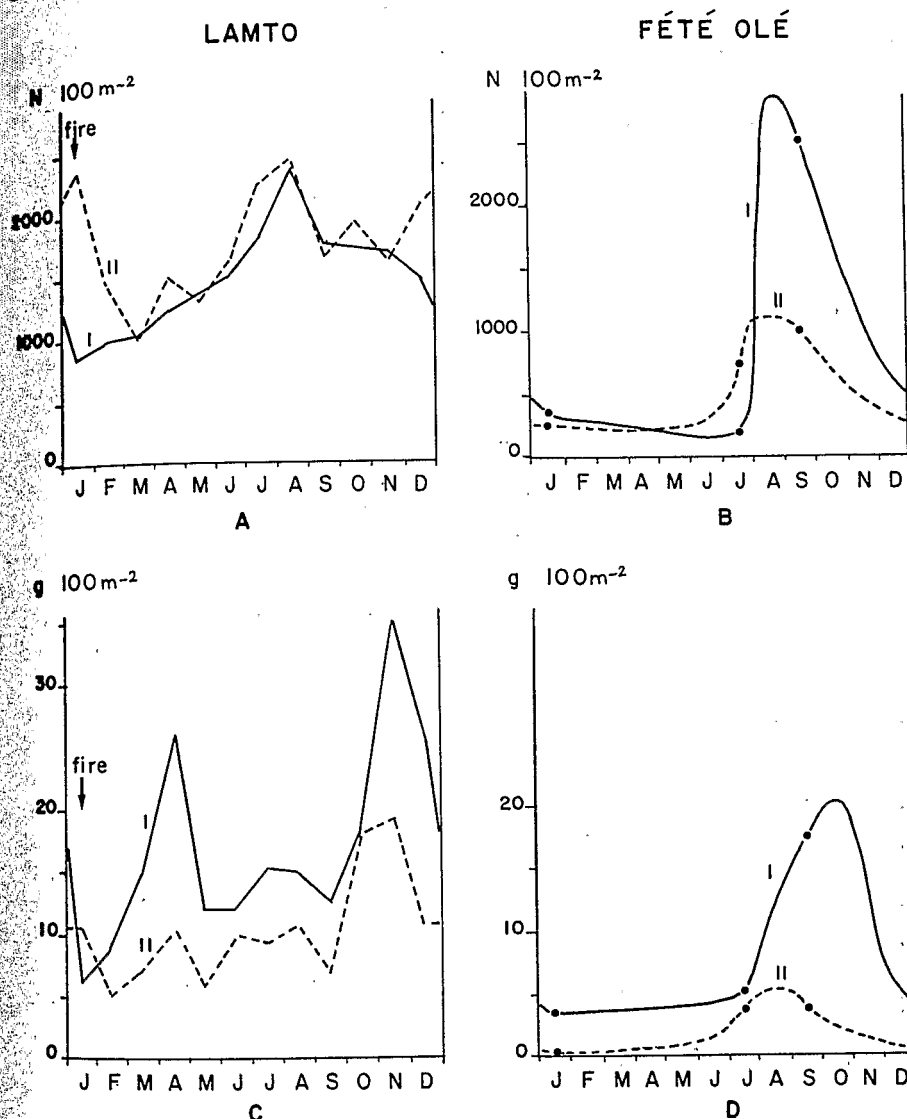LAMTO   FÉTÉ OLÉ

Fig. 11.8. Seasonal variations of the numbers (upper graphs) and biomasses (lower graphs) of arthropods in two African savannas, the Guinean savanna of Lamto, Ivory Coast (the two graphs on the left side of the figure) and the Sahelian savanna of Fété Olé, Senegal (on the right side of the figure). Primary consumers (*I*) and secondary consumers (*II*) are figured separately. The same sampling techniques were used in the two cases. Biomasses are expressed in dry weight per 100 m². (After D. Gillon and Gillon, 1974.)

so at the end of the rainy season (*Firmicus hay-woodae, Proxysticus egenus*; Fig. 11.9).

Species belonging to a single genus can display different phenologic cycles: adults of *Tibellus seriepunctatus* are found from April to June, while those of *T. demangei* are found from August to November. Univoltine and multivoltine spiders can also be found within a same genus: *Thanatus dorsilineatus* has a single breeding season, whereas *T. lamottei* and *T. pinnetus* are bivoltine.

Protracted life-cycles can result from a slow post-embryonic development. *Runcinia sjoestedti* and *Tibellus seriepunctatus* hatch in September and October, and reach the adult stage six to seven months later; these spiders spend the dry season as juveniles. Conversely, *Diaea puncta* hatches in January, at the peak of the dry season, whereas the last adult individuals have disappeared months earlier; in this case, it is the embryo which develops slowly or undergoes an embryonic diapause. On the

TABLE 11.4

Seasonal fluctuations in insect numbers and biomass in sweep samples from the Athi Plains, Kenya (after Dingle and Khamale, 1972)

		Number of species	Number of individuals	Standing crop biomass (mg dry wt.)
October	1969	87	204	1161
November	1969	117	561	1160
January	1970	127	1002	901
March	1970	102	791	1315
May	1970	214	1133	4162
July	1970	121	994	1432
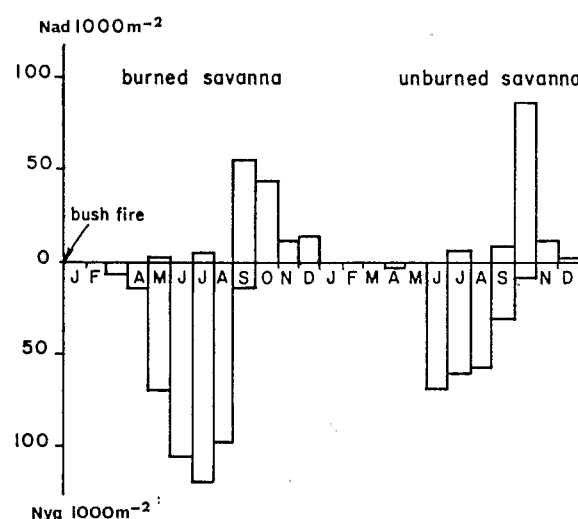
Fig. 11.9. Seasonal variations in numbers of the spider *Firmicus haywoodae* (Thomisidae) in the Lamto savanna. The number of adult individuals (*Nad*) are indicated by the top histograms, and the immatures (*Nyg*) by the bottom histograms. (Data from Blandin, 1972.)

other hand, the post-embryonic development of *Diaea puncta* is twice as fast as that of the preceding species. So far, no adult diapause stage is known for these Lamto spiders.

The invertebrate group having the most clearly understood life cycle in tropical savannas is the acridids. Their univoltine species either enter diapause at the embryonic stage or as adults. Such univoltine acridids are always very numerous in the savanna communities studied (Phipps, 1968). Out of a total of 76 species studied by Lecoq (1978a) in the Saria area, Upper Volta, where the annual rainfall is only 836 mm with a single long dry season between the middle of October and the end of May, 50 species (66%) are univoltine. This is the

same percentage as that found by Y. Gillon (1974) at Lamto, much further south, where the average annual rainfall is over 1200 mm and the short dry season is far less severe. Among the 23 species whose life-cycle has been studied at Maradi, Niger, by Launois and Launois-Luong (pers. comm., 1979), twelve were univoltine, four bivoltine and seven trivoltine.

The ovaries of the acridid females undergoing an imaginal diapause during the dry season remain at a very early stage of development (pre-vitellogenesis) during the drought, and sexual maturity coincides with the onset of the first rains. The triggering of sexual maturation can be very rapid, as in *Acridoderes strennus* at Saria, where it takes place as soon as the atmospheric moisture begins to increase, in April. The first eggs are laid in June (*Acorypha clara, Tylotropidius gracilipes*) and the adults are found from early September (*Catantops axillaris*) to early December (*Rhabdoplea munda*), with a peak in October when the grass cover reaches its maximum standing crop (Lecoq, 1978a).

Incidentally, *Rhabdoplea munda* raises a very intriguing problem. At Saria, all individuals belong to the macropterous form, only one micropterous individual having ever been found by Lecoq (pers. comm., 1979). Further south, in the Lamto Guinean savanna, the situation is different, only half of the individuals belonging to the dry-season generation are macropterous, the others being micropterous. In the lowland rain forest of West Africa, most acridid species are also micropterous.

When diapause occurs at the egg stage, it takes place before blastokinesis (Dempster, 1963). Whereas the eggs of *Zonocerus variegatus* begin to hatch in May, at Saria, those of *Orthochtha grossa* do not do so before August, at a time when most

sympatric species have already reached their adult stage. Female *Orthochtha grossa* do not lay their eggs before October, at which time most other sympatric acridids become adult before entering diapause during the dry season (Lecoq, 1978a).

In the Lamto area, the eggs of univoltine acridid species begin to hatch in early March [*Acorypha johnstoni*, *Chloroxyrrhepes virescens* (Fig. 11.10) and *Dnopherula bifoveolata*]. Of the three short-horned grasshoppers just mentioned, the first two undergo an embryonic diapause and the last experiences an adult diapause. Other univoltine species continue to hatch until the end of May (*Bocagella acutipennis*, *Dictyophorus griseus*,

Machaeridia bilineata and *Tanita parva*, all undergoing adult diapause). Young *Eucoptacra anguliflava* hatching at that time of the year can come from eggs laid either before or after the dry season, adults being found throughout the year.

Two Lamto species, however, undergo diapause during the rainy season, which incidentally implies that it cannot be considered the most favourable period for all species in this taxonomic group. *Petamella prosternalis* eggs are laid at the onset of the rains, but do not hatch before August or September (Fig. 11.11), thus implying a rainy season embryonic diapause, as defined by Phipps (1968). On the other hand, *Gastrimargus africanus* enters diapause at the adult stage.

If the hatching time of all univoltine species studied in different parts of West Africa are compared, it becomes apparent that there are always some species which hatch before or after the main hatching period of most of the others (Fig. 11.12). The hatching of half of the sympatric species is
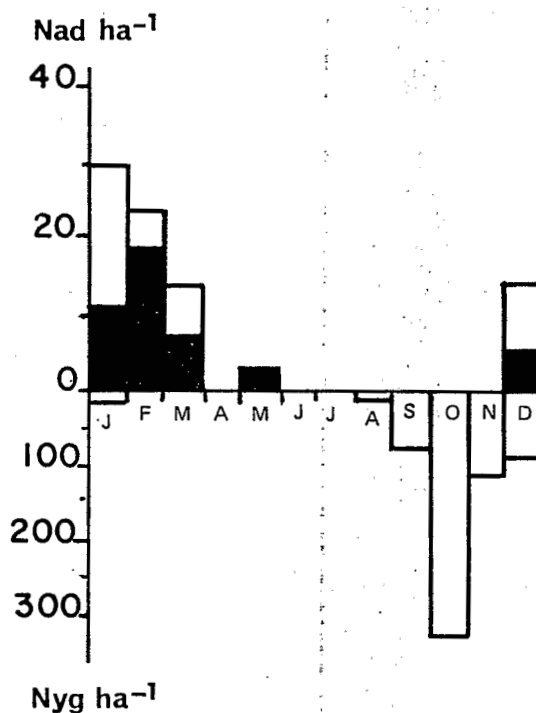

Fig. 11.10. Seasonal variations in numbers of young (*Nyg*, bottom histograms) and adult (*Nad*, top histograms) of *Chloroxyrrhepes virescens* (Acrididae, Tropidopolinae) in the Lamto savanna; an example of embryonic diapause and early hatching. Females in black. (After Y. Gillon, 1974.)

Fig. 11.11. Seasonal variations in numbers of young (*Nyg*, bottom histograms) and adult (*Nad*, top histograms) of *Petamella prosternalis* (Acrididae, Tropidopolinae) in the Lamto savanna; an example of adult diapause with late hatching. Females in black. (After Y. Gillon, 1974.)
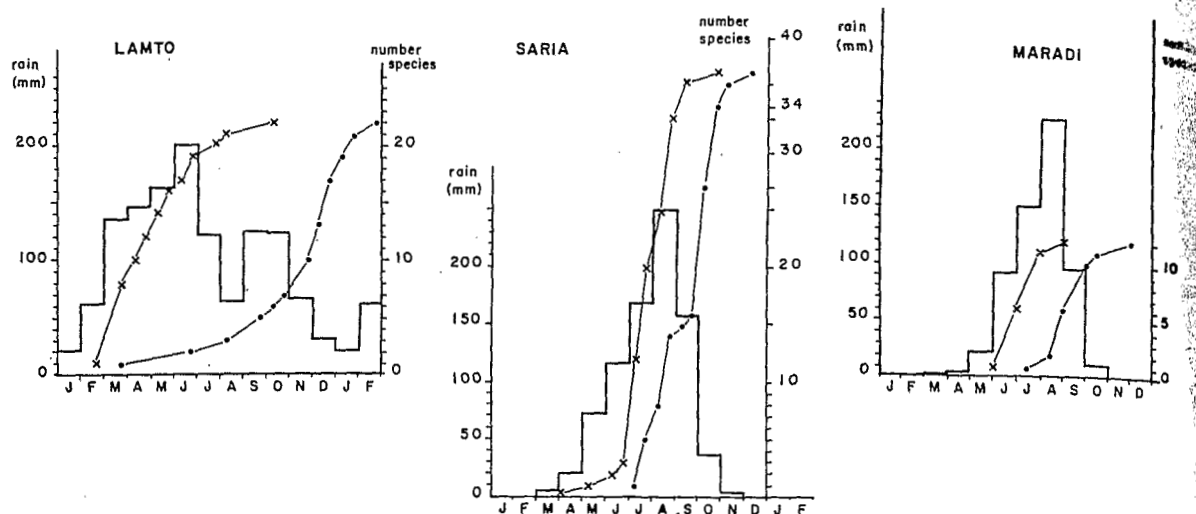
Fig. 11.12. Fifteen days summation of the number of acridid species breeding once a year, at the time of hatching (X) and of complete development (●), in three different West African savanna study sites, Lamto (Ivory Coast), Saria (Upper Volta) and Maradi (Niger). The histograms represent the average monthly rainfall. (Based on data by Gillon, Lecoq and Launois Luong.)

completed at different times of the year in different localities, but always at the end of the second month of the rainy season in the three study sites concerned. According to Lecoq (pers. comm., 1979), the bend of the hatching graph separates the species with an embryonic diapause, and those undergoing an early imaginal moult, from those with a late imaginal moult. In all three cases, the latest hatchings occur long after the beginning of the emergence of the early hatching species.

Seasonal variations in numbers of multivoltine acridid species

The case of the acridid *Rhabdoplea munda*, previously described, shows that the number of breeding generations per year for a given species can vary in different parts of its range. The same thing happens in multivoltine species living in different environments. *Oedalus senegalensis*, for example, can breed once, twice or three times annually, not only in different localities, but also in the same area, depending upon the yearly environmental conditions (Batten, 1969; Launois, 1978b). In this case the number of broods per year is higher in more humid conditions. The reverse can also occur, however; *Eucoptacra anguliflava* and *Gastrimargus africanus* have only one generation per year at Lamto, Ivory Coast, against two and three re-

spectively in the drier savannas of Upper Volta. The population turnover of these two acridids is apparently slower in what one might consider to be a more favourable environment. Working with crickets in Japan, Masaki (1978) has shown how complex the determinism of latitudinal variation on the annual number of generations is, involving as it does a subtle interplay of genetic and ecological variables.

Large size acridids are generally those whose life-cycles are the longest, about a year, involving an embryonic diapause. A large locust which has several generations annually implies an unusual ability to synthesize living tissues and to metabolize a considerable amount of food. Such is indeed the case for *Locusta migratoria* and *Schistocerca gregaria* which devastate natural and cultivated vegetation when they feed.

The most important synchronizer of the major stages of the life-cycle, hatching particularly, is the occurrence of the first rains at the end of the dry season, as established by Louveaux (1972) in *Locusta migratoria* in the Malagasy grasslands.

Seasonal variations in numbers of savanna pentatomids

Univoltine species are rare among the small-size pentatomids of the grass layer in West African wet

savannas. At Lamto, only one single brooded species (*Deroplax nigropunctata*) out of a total of fifteen, has been found by D. Gillon (1974). Mating takes place in October, followed by the death of the males, and laying occurs in November and December (Fig. 11.13). Young stages of *Deroplax nigropunctata* develop during the dry season, and an imaginal diapause takes place during the rainy season. All the other sympatric species of pentatomids are multivoltine, with an inactivity period during the dry season. *Ennius morio* for instance, has two distinct breeding generations with population peaks in June and November, the beginning and the end of the rainy season (Fig. 11.14).

To summarize, the life-cycle of sympatric heterometabolous insects in a given savanna can be extremely variable, even within one univoltine species. However, definite population peaks can be observed in West African savannas, both at the
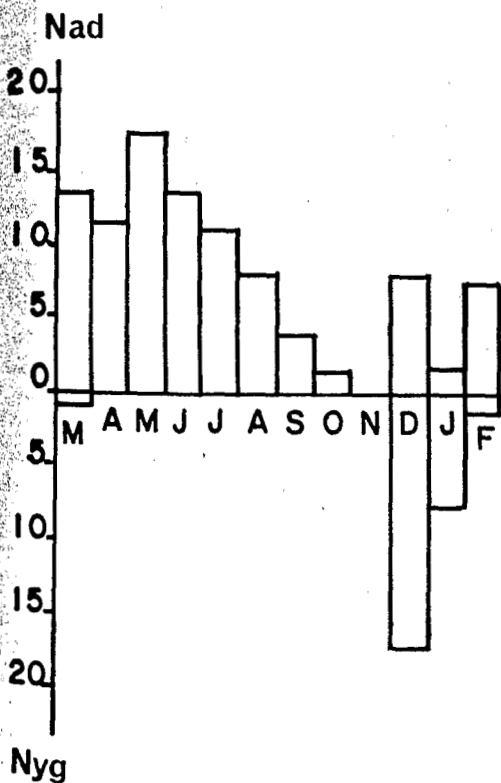

Fig. 11.14. Seasonal variations in numbers of young (*Nyg*, bottom histograms) and adults (*Nad*, top histograms) of *Ennius morio* (Pentatomidae, Pentatominae) in the Lamto savanna. (After D. Gillon, 1973.)

Fig. 11.13. Seasonal variations in numbers of individuals per 1000 m^{-2} of young (*Nyg*, bottom histograms) and adults (*Nad*, top histograms) of *Deroplax nigropunctata* (Pentatomidae, Scutellerinae) in the Lamto savanna. (After D. Gillon, 1973.)
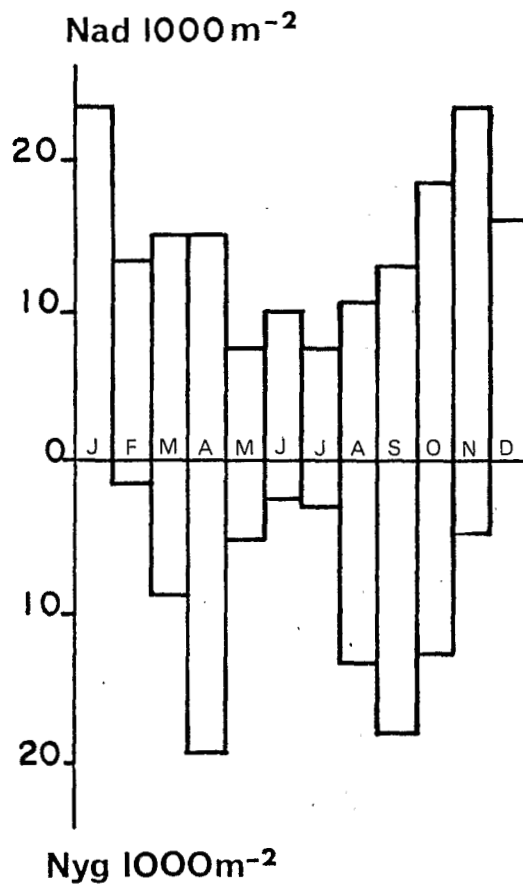
onset and at the end of the rainy season, as noticed long ago by Lamotte (1947).

Seasonal variations in numbers of holometabolous insects

The seasonal variations in abundance of holometabolous insects are poorly understood in tropical savannas, because the study of their population dynamics involves different sampling techniques for larvae, pupae and adult individuals. Nevertheless, the abrupt increase in the numbers of most butterflies and moths at the beginning of the rainy season implies a synchronizing role (direct or indirect) of the first rains, as in the case of heterometabolous insects. However, many species also

have a second breeding generation at the end of the rainy season.

Adult holometabolous insects are often long-lived. Some carabid beetles can live for a year at Lamto (Lecordier et al., 1974), and tenebrionid beetles can live for several years (Y. Gillon and Gillon, 1974). It is therefore difficult to establish the number of breeding generations, and it becomes necessary to study both the seasonal variations in the larval populations, and the breeding behaviour of the adults. In the case of the rutelid beetle *Anomala curva* studied by Girard and Lecordier (1979) at Lamto, adults occur nine months out of twelve, but the duration of the larval stage is less than six months. Adults are more often seen flying around from February to April and from September to November. Two breeding generations are therefore likely, especially since all the other sympatric rutelid species are least often captured in light traps at the peak of both the rainy and dry season (Fig. 11.15). But the situation may be further complicated by differences between adjacent micro-habitats within the same savanna landscape. In pure Lamto grassland the density of adult *Anomala curva* exhibits two peaks in abundance (in February and in October) in the upper layer of the soil where they take shelter outside their periods of flying activity. But the populations sampled at the base of *Borassus* palms, whether in the middle of the savanna or near the forest edge, show a single peak in June or July (Fig. 11.16).

Fig. 11.16. Seasonal variations in numbers of rutelid beetles per 1000 m^2 in different micro-habitats of the Lamto savanna: in the open grassland (heavy line), at the bottom of *Borassus* palm (dashed line), and at the forest edge (dotted line). Histogram: the rains in the background. (After Girard and Lecordier, 19?)

Generally speaking, polyvoltine species have a better reproductive potential than univoltine species, and some also benefit from the adaptive advantages of seasonal delays in development. In these species, diapause and quiescence are apparently not under strict genetic control, but are triggered by external synchronizers. Unfortunately, very little is known about these timing devices in tropical latitudes; the seasonal variations of photoperiod are very limited, and the onset of the first rains alone is a highly unreliable predictor of the rainy season, at least in the drier (Sahelian) savannas.

To complicate the issue further, the breeding of many species under laboratory conditions has disclosed the frequency of polymorphism among savanna insects, as well as the frequent occurrence of an overlapping of generations.

Bivoltine butterfly species can be represented by different forms at different times of the year. The wet season form of the nymphalid *Precis octavia* is bright orange with black markings, while the dry season form is intricately patterned with dark markings and blue spots and has almost no orange. In this case, rainfall and humidity, rather than temperature, are considered as the main stimulus affecting the production of these seasonal forms (Owen, 1971, 1976). Some satyrid butterflies which have quite distinct wet- and dry-season forms in the Sudanian savanna, also have intermediate forms (Fig. 11.17) in the Guinean savanna of the Ivory
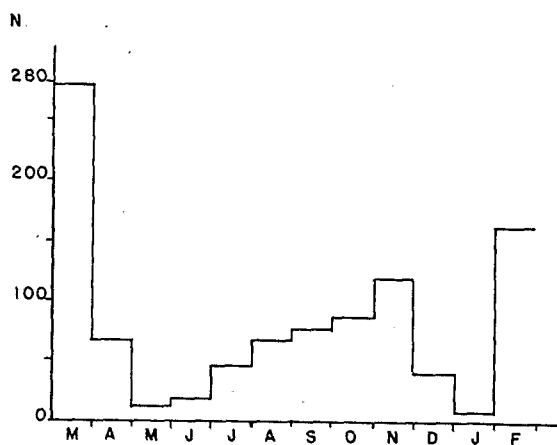

Fig. 11.15. Seasonal changes in above-ground activity of rutelid beetles in the Lamto savanna, based upon the number of individuals caught in light traps. (After Girard and Lecordier, 1979.)
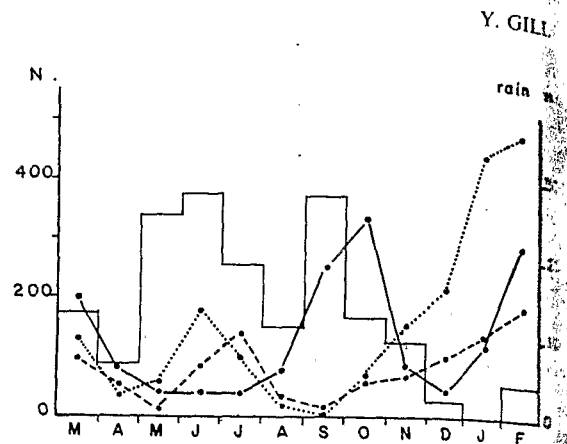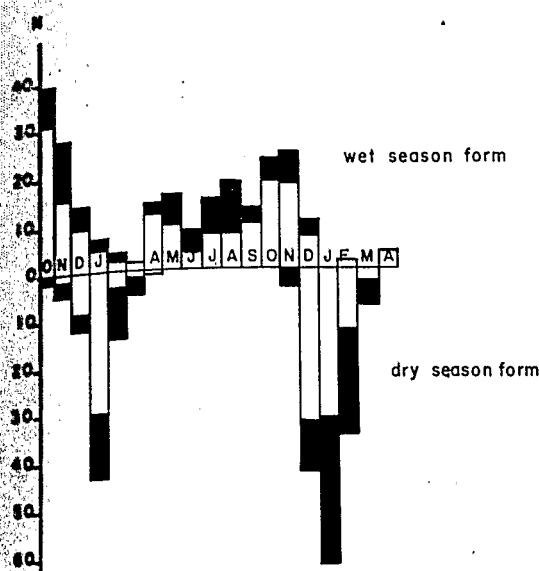
Fig. 11.17. Seasonal variations in numbers of the butterfly *Bicyclus milyas* (Satyridae) in the Lamto savanna. Females are indicated in black for both the rainy-season form (top histograms) and the dry-season form (bottom histograms). (Data from Condamin and Vuattoux, 1972.)

Coast, further south, where seasonal conditions are less contrasted (Condamin and Vuattoux, 1972). In many cases males outnumber females, the latter developing more slowly. In Guinean savannas where the dry season is short, dry-season forms appear much more quickly than the wet-season forms, as shown by *Bicyclus milyas* at Lamto (Fig. 11.16).

THE SEASONAL MIGRATIONS OF SAVANNA INSECTS

One of the major differences between the insect fauna of wet and dry savannas is the lower incidence of seasonal migrations in the former *versus* its frequent occurrence in the latter. In the Guinean and more humid savannas, often interspersed with gallery forests (the forest savanna mosaic), the seasonal variations of climate are far less marked and much more predictable than in the drier savannas. Furthermore, in the latter situation, the seasonal movements of the intertropical convergence zone carry with them a large number of adult insects adapted to long-range movements.

Acridid migrations

It is noteworthy that acridids from the dry savanna areas are far more mobile than those of the wet savannas. They are much more prone to be captured in light traps, especially because their activity peaks take place during the night. Clark (1969), for instance, has described the night movements of the Australian plague locust *Chortoicetes terminifera* in relation to storms. At Maradi, Niger, Launois (1978b) has also found a positive correlation between the number of *Oedaleus senegalensis* caught in light traps and temperature. The ability to move over long range is correlated with obvious morphological characteristics. Out of the 103 species of acridids studied by Launois (1978b) in the Sudanian and Sahelian savannas of West Africa, only a few species of *Chrotogonus* belonged to the micropterous form, whereas 10 out of the 101 species of the Lamto Guinean savanna had micropterous females, according to Y. Gillon (1973b). It has already been mentioned that almost all *Rhabdoplea munda* individuals are short-winged in the Guinean savanna of the Ivory Coast during the rainy season, whereas the long-winged form is the rule in the Sahel. This is not to say that seasonal movements do not occur among wet savanna acridids; they do, but far less frequently. In the Ivory Coast, *Ornithacris turbida* and *O. magnifica* probably follow the harmattan during the dry season, entering the Sudanian savannas of West Africa at that time; if this were not so, it would be difficult to understand why the young instars of these species are far less numerous than the adults in these areas (Y. Gillon, 1973b).

The seasonal changes in demographic structure of *Oedalus senegalensis* populations at Saria, Upper Volta, have enabled Lecoq (1978a) to establish arrival and departure schedules for this insect in the area (Fig. 11.18). The numbers of first-generation adult individuals falls sharply in June, before the maturation of ovaries in the females. This outward movement corresponds to the northward movement of the intertropical convergence zone. Four months later, adult females of the third generation suddenly appear in numbers, this inward movement coinciding with the southward movement of the intertropical convergence zone, at the end of the rains. Similar observations have been made on *Catantops haemorrhoidalis* in the same area
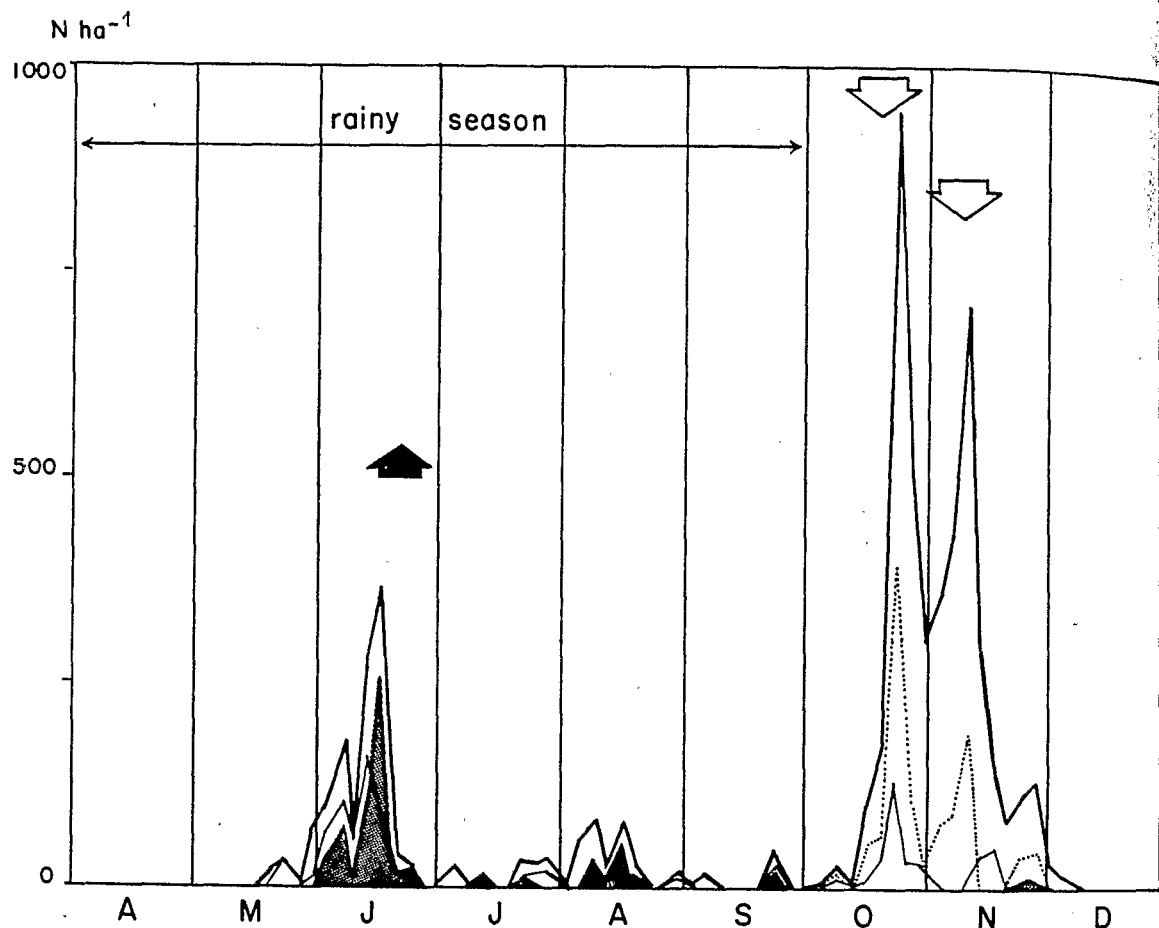
Fig. 11.18. Frequency of occurrence of *Oedalus senegalensis* at Saria, Upper Volta. Heavy line: overall population density; hachure: females with soft cuticle; thin line: non-breeding females with hard cuticle; dashed line: breeding females. The black vertical arrow indicates the departure of adults, and the two white arrows the arrival of other adults. (After Lecoq, 1978a.)

(Duranton et al., 1979). Therefore, the beginning and the end of the rains play as decisive a role in triggering mass population movements as they do in initiating breeding among insect communities of these savannas.

Direct observations by radar operating at ground level (Schaeffer, 1976; Reynolds and Riley, 1979a,b), or from aircraft (Rainey, 1975), have provided much information on the altitude, direction and importance of insect flights. It has even been possible to capture some flying individuals within the night swarms, using nets towed by slow-flying planes. Even species long considered as sedentary and solitary, such as *Aiolopus simulatrix* and *Catantops axillaris*, have been captured in this way (Schaeffer, 1976). The build-up of these

swarms takes place progressively, and probably increases the opportunity for mating (Rainey, 1976). This might particularly be the case when swarming occurs regularly in well-defined localities, such as large river valleys in Mali (Reynolds and Riley, 1979a).

Among true migratory locusts the crowding together of many young nymphs results in increased activity, which in turn is associated with the development of morphological characteristics of a gregarious phase. Such a gregarization process results in the well-known locust plagues. In savanna areas plague locusts are represented by several species of *Anacridium* and *Nomadacris*, which feed mostly on trees and shrubs, as well as by *Schistocerca americana* in the New World and

Schistocerca gregaria and *Locusta migratoria* in the Old World. Of these last two species, the former is most frequent in sub-desertic areas, and the latter in Sahelian savannas, reaching North Africa and even southern Europe on rare occasions. The gregarious phase of *Locusta migratoria* has its outbreak area in the flood plains of the middle Niger Valley, from where its swarms invade large regions.

Solitary phase individuals of this species, however, can also undertake large-scale movements, possibly enabling four different generations to follow one another in the course of a year. Eggs are laid during the dry season in the south of the outbreak area, as soon as the floods recede; they give rise to adults which move northward and breed there. The next generation lays its eggs at the onset of the rains, and the third generation moves further north during the short rains; it is the adults of the fourth generation which move back towards the south.

A similar succession of four generations in solitary *Locusta migratoria* has also been described in southwest Madagascar by Lecoq (1975). The largest individual flight range recorded among colour-marked solitary locusts is 300 km (Davey, 1956, 1959).

Air movements usually carry locusts towards low-pressure areas, where the occurrence of rainfall is the most likely, thus optimizing their reproductive success and the chances of survival of the first instars.

Migrations of the cotton stainers (*Dysdercus* spp.)

Long-range migratory movements are also well known among other savanna insects: the army-worms, caterpillars of the noctuid moth *Leucania loreyimpuncta*, and the cotton stainers — pyrrhocorid bugs belonging to the genus *Dysdercus*, which feed upon the seeds of Malvales.

The long-range movements of cotton stainers had already been suspected by Golding (1928) in Nigeria, but a more comprehensive study of *Dysdercus voelkeri*, carried out in Ivory Coast by Duviard (1977), threw a new light on the problem. Two kinds of large-scale seasonal movements were identified: (1) a dry-season invasion of Guinean savannas, the southernmost part of the species' range, during which great damage is done to cotton fields; and (2) an early rainy-season migration in the Sudanian savannas, the northernmost part of the *D. voelkeri* range. This migration has not been given much attention in the past, since it causes far less damage to crops (Sarel Whitfield, 1933).

These seasonal movements are accompanied by a change in colour of the insects. Those moving south are yellow in colour; in Guinean savannas they give rise to a new generation whose adults are red. This generation in turn produces orange individuals at the beginning of the rains before disappearing for good from the Guinean savannas, at the same time that their staple food, the seed of Malvales, becomes unavailable. Most of the rainy season migrants in the Sudanian savannas are also orange-coloured, but their local progeny is yellow — the very colour of the bugs moving south later on with the intertropical convergence zone.

Duviard's interpretation of the seasonal movements and colour changes of *D. voelkeri* explains the observed facts better than the alleged short-range movements between cotton fields and wild host-plants postulated by Pearson (1958).

In moving seasonally between two adjacent savanna zones, *D. voelkeri* populations actually manage to maintain themselves in a very stable climatic environment: the dry season in the Guinean savannas, which is so frequently interspersed with showers, does not differ much, in fact, from the rainy season in the Sudanian savannas.

The "natural marking" of *D. voelkeri* generations might itself be due to seasonal changes in illumination, a more intense light turning red pterines into yellow ones. Vuillaume (1969) has indeed described the influence of solar radiation upon the synthesis of chromoproteins.

The possible role of a dietary change is far more questionable; the body colouring of the adults is achieved before they start feeding (Duviard, 1977). Moreover, the first meal of an adult female coincides with the end of its ability to undertake large-scale, and even small-scale movements, its flight muscles being more or less destroyed by histolysis (Edwards, 1969). Group living might also play a role at this stage to reinforce the effect of feeding (Gatehouse and Hall, 1976). Immigrant females cannot become sexually mature before beginning to feed, and mating also stimulates both muscular histolysis and ovarian maturation.

The circumstances of migrating flights

The flight periodicity, direction and range of migrating swarms of a few savanna insects are now adequately documented. Yet very little is known on the conditions of these long-range movements.

For an insect to benefit from an air current means that wind velocity must at least be the same as the velocity this insect reaches in active flight. Schaeffer (1976) indeed recorded that locust swarms tracked by radar had an average speed of 3 m s^{-1}, and that flight duration averaged three hours — figures well in line with the performances of insects flying in laboratory conditions.

To take advantage of the kinetic energy of a low-level jet stream, the migrating insect first has to reach a certain elevation, as the lower levels of air move very slowly or not at all. To do so, it must first cross the boundary layer — that is, the layer of air near the ground within which insects are able to control their movements relative to the ground because their flight speed exceeds wind speed (Taylor, 1974).

The directions followed by insects at take-off are not very meaningful; environmental conditions such as light intensity, air temperature, atmospheric moisture and barometric pressure are more significant. They play a definite role in the initiation of upwelling air currents (thermals). Some indications of the optimal conditions for night migration can be drawn from the results of light-trapping; more insects are generally caught in pitch-dark nights, although giant water ' bugs (Belostomatidae), *Diplonychus nepoides* particularly, prefer full moon nights (Duviard, 1974). It is possible that they are attracted by the reflexion of moonlight on the savanna pools (Cullen, 1969).

As mentioned earlier, large-scale migratory movements often take place at the turning points between the dry and rainy seasons. This is why it is best to conclude, at least in West Africa, that the four significant periods in the annual cycle are: first, the dry season; then, the tornado period corresponding to the advance of the intertropical convergence zone; third, the rainy season; and fourth, the retreat of the intertropical convergence zone. The "short dry season" occurring in the middle of the rains in subequatorial climates does not appear to have much phenological importance in Guinean savannas.

All locust migration circuits result in swarms moving in a direction which is most likely to take them to the area containing the most suitable habitats for that particular season. Some swarms however, can be led by strong winds in a wrong direction to perish *en masse* in the sea. There are many instances of swarms of *Schistocerca gregaria* ending up in the Red Sea, and similar incidents have been recorded for other migratory species: *Chortoicetes terminifera* in Australia (Farrow, 1975) and *Zonocerus variegatus* in the Ivory Coast (Duviard, 1977).

CONCLUSIONS

In spite of the many differences found among the arthropod faunas of the various categories of savannas, some basic similarities do exist which confer a pattern common to all of them, at least in Africa.

First of all, the ubiquity of acridids, which together with caterpillars during the rainy season make up the major groups of primary consumers. It might well be that in some cases their trophic impact on the vegetation is more important than that of grazing mammals.

Among secondary consumers, the same dominant role is played by spiders and ants (see Ch. 24). In West African savannas four families of spiders represent 60 to 80% of the total number of spiders present, both at Lamto and at Fété Olé (D. Gillon and Gillon, 1974; Blandin, 1974).

Most of the major faunal differences between dry and wet savannas are due, at least in Africa, to other taxonomic groups: Solifuga, scorpions, Thysanura, Embioptera and tenebrionid beetles are true faunistic "markers" of the driest savannas, whereas Phalangida, cockroaches, tetrigids and tridactylids are always scarce, if not absent, in such habitats. The dichotomy between the more seasonal savannas and those closer to the forest edge is even more marked during the dry season; at that time of the year some groups, such as jassids or carabid beetles, and some life stages such as caterpillars, are no longer active though present during the rainy season.

The second common characteristic of all arthropod faunas in savanna ecosystems is the high prevalence, at the individual as well as at the

population level, of adaptive mechanisms which help the species to avoid the most drastic conditions of the dry season. Such "escape strategies" take advantage of a wide range of morphological, physiological and behavioural adaptations which permit the animals either to spend the dry season in a more or less torpid stage, or to move away from the sun-parched grass to more congenial environments, some centimetres below the ground or hundred of kilometres away.

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ECOSYSTEMS OF THE WORLD 13

Vol.: ## TROPICAL SAVANNAS

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Université René Descartes
45, rue des Saint-Pères
Paris (France)

ELSEVIER SCIENTIFIC PUBLISHING COMPANY

Amsterdam — Oxford — New York 1983