The Effect of Bush Fire on the Principal Pentatomid Bugs (Hemiptera) of an Ivory Coast Savanna

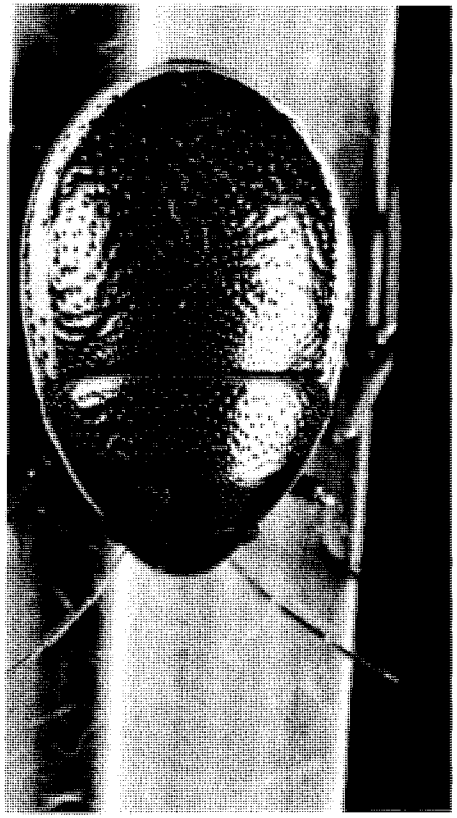
DOMINIQUE GILLON

Laboratoire d' Entomologie, Office de la Recherche, Scientifique et Technique Outre-Mer, Centre D'Adiopodoumé, B. P. 20, Abidjan, Republique de Côte d' Ivoire

(Translated by Victoria Tschinkel, Tall Timbers Research Station.)

CHARACTERISTICS OF THE REGION UNDER STUDY

This research was carried out on the savanna in the neighborhood of the Lamto Tropical Ecology Station at 6° north latitude. The climate is of the humid tropical type with a semi-dry season from November to February followed by a wet season from March to October. These savannas are characterized by grassy borassus palm (*Borassus aethiopum*) areas separated by gallery forests that line the water courses. The pentatomids live mainly in the herbal layer, composed mostly of grasses, *Hyparrhenia* spp. and *Loudetia simplex.*



1. *Cyptocoris lundi*, female. This sci-
is species becomes twice as abundant
he area is not burned.

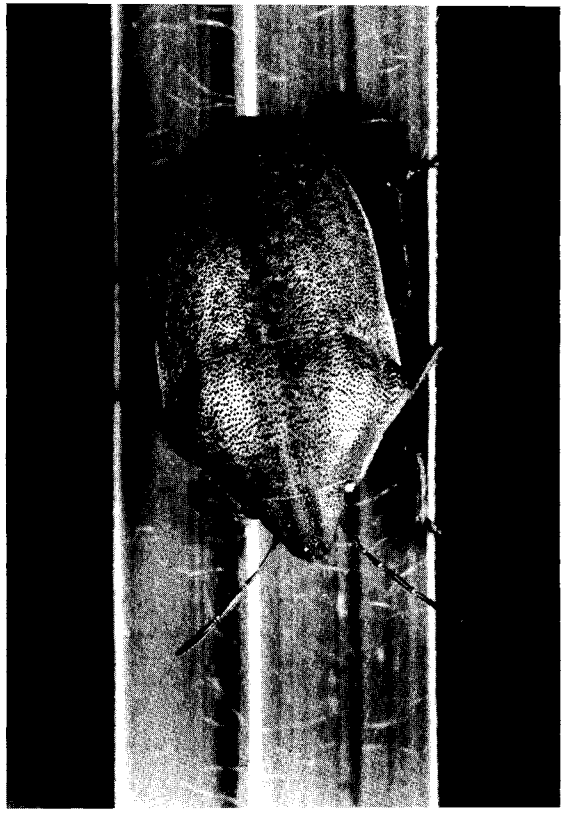
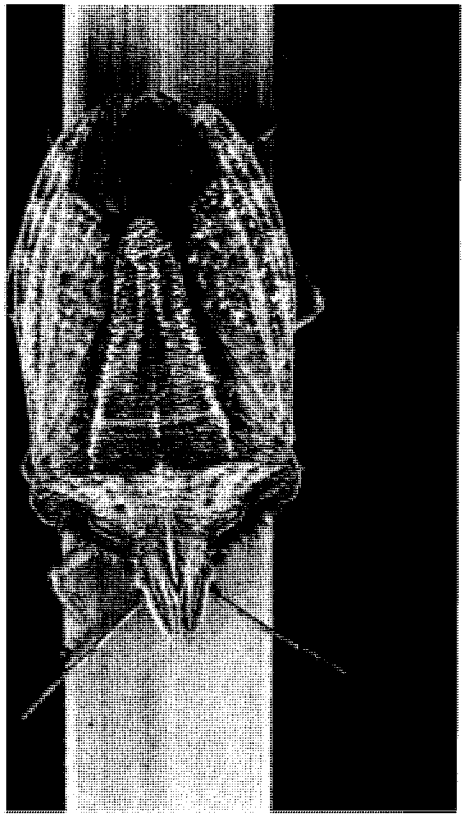


FIG. 2. *Deroplax nigropunctata*, male. A sciaphilous species that becomes five times more abundant in unburned savanna than in burned savanna.

FIG. 3. *Dichelorhinus vittatus*, female. A heliophilous species preferring the burned savanna, which becomes four times more abundant than in unburned areas. This female has molted and left behind its exuvie. The integument is clear and soft, later becoming darker and harder.



4. *Lobopeltista guineensis, male.* A heliophilous species which recovers slowly in the savanna.

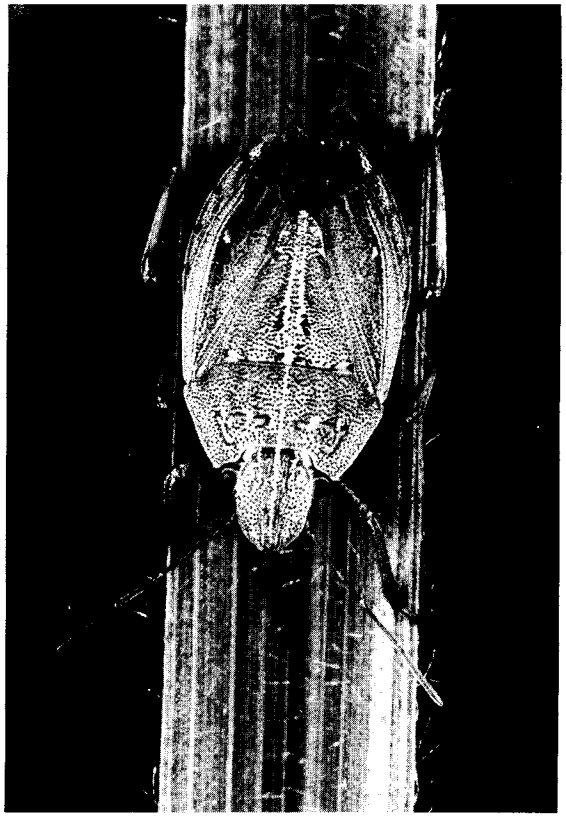


FIG. 5. *Dymantis grisea,* male. A widespread, heliophilous, and mobile species, clearly dominant in the burned savanna, frequently also in the unburned savanna.

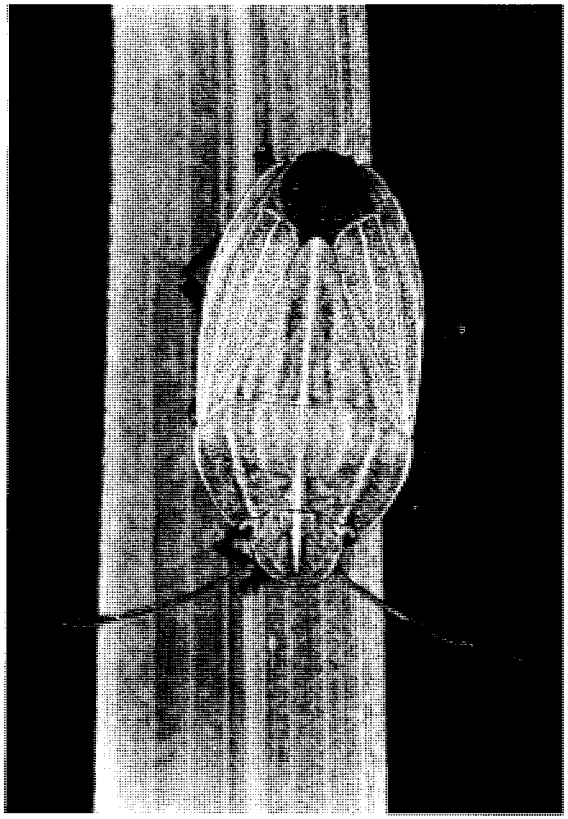


FIG. 6. *Delegorguella phalerata,* male. This is the only heliophilous species dominant in the unburned savanna, and is completely eliminated by the passing fire.

CHARACTERISTICS OF THE PENTATOMID POPULATION

For a proper understanding of the effects of fire on the savanna pentatomid bug population, it is essential to distinguish between the two types of behavior observed in these insects. Certain heliophilous (sun-loving), mobile species live on the erect vegetation while the sciaphilous (shade-seeking) species live at soil level in the center of the grass tufts. There are also apterous pentatomids, all the nymphs and the adults of *Aeptus singularis* (Table 1) (Figs. 1–6).

With the exception of *Deroplax nigropunctata*, which reproduces during the dry season, the pentatomids' annual cycle is directly tied to that of the rains. The first generation of young appears at the beginning of the rainy season, and then several successive generations appear during the rest of the rainy season, from April to November. The adults of the last generation of the year spend the dry season,

TABLE 1. LIST OF THE MAIN SPECIES OF PENTATOMIDS

GRAPHOSOMATINAE
- *Cyptocoris lundi* (Fig. 1)
- *Oncozygidea flavitarsis*
- *Thoria rotundata*
- *Thoria gillonae*
- *Sepidiocoris dispar*[1]
- *Sepidiocoris noualhieri*[1]

SCUTELLERINAE
- *Deroplax nigropunctata* (Fig. 2)

DINIDORINAE
- *Cyclopelta funebris*

PHYLLOCEPHALINAE
- *Dichelorhinus vittatus* (Fig. 3)
- [2]*Gonopsis reuteri*
- *Gellia dilatata*
- [2]*Gellia punctulata*
- *Lobopeltista guineensis* (Fig. 4)
- *Sandehana labiosa*

PENTATOMINAE
- *Aeptus singularis*
- *Dymantis grisea* (Fig. 5)
- [2]*Dymantis plana*
- *Delegorguella phalerata* (Fig. 6)
- *Ennius ater*
- *Ennius morio*
- [2]*Halydicoris kraatzi*
- *Aeliomorpha divisa*
- [2]*Eusarcoris purpurissatus*
- *Actuarias varians*
- [2]*Menida maculiventris*

[1] The nymphs of the two species of *Sepidiocoris* are indistinguishable.
[2] Less abundant species, not among those comprising 90 percent of the population.

from December to March, in reproductive abeyance, and do not lay eggs until the first big rains in March–April. The length of one generation varies from one species to another, but never exceeds 4 months. Thus, there are always at least two generations a year. In August, there is a respite in the middle of the rainy season which justifies its separation into a first and second rainy season. This lessening of the rain often corresponds to the end of one generation, and the beginning of another, thus diminishing the effective number of pentatomids at this time.

FIRE

Like climatic factors, fire is one of the main influences governing the development of the savanna (Figs. 7 and 8). It is easily submitted to experimentation by suppression or by changes in its time of application with the object of determining specific effects.

Fire is started by the local inhabitats each year, usually in the dry season. The essential characteristic of fires in this region is that their spread is inevitably restricted by the permanently humid climate and the existence of the gallery forests. Thus the whole region is never on fire at any given time. Areas not burned in 1 year have a greater chance of burning the following year because of their accumulation of dry grass.

The fire advances at an average of 500 m/hour, giving the more mobile animals chance to escape, but its velocity and intensity vary greatly according to the speed and direction of the wind, the density and type of the vegetation, and the prevailing weather conditions.

Temperatures vary with the topography, the highest (600°C) having been observed at a height of 20 cm in herbaceous vegetation. At soil level they are variable: from 75°C to 350°C with only a few degrees rise in the interior of the bases of the clumps of grass, or beneath a thin crust of earth. The arthropods seek refuge from the fire under stones, in holes and cracks in the soil, in the dense base of the grass clumps, in fact anywhere that offers the slightest shelter. At the interior of grass tufts, Jeager and Adam (1967) recorded temperatures of 50°C during passage of fire in Sierra Leone. Thus, spectacular, fire is not very destructive at the level at which the insects live.

FIG. 7. The savanna before the fire. Contrast this with Fig. 8: two entirely different habitats.

Monnier (1968) studied the effects of fire on the habitat. Nothing is left of the thick, meter high plant cover except the bases of grass clumps (the centers of which do not burn), a little upright stubble, and a layer of light ash which is quickly dispersed by the wind or washed into the soil by the first rains.

Regrowth is rapid; the young green leaves begin to appear a few days after the fire. In a month they are 10 cm high and cover 40 percent of the ground. This regrowth accelerates with the early rains in March. Four months after the fire there is 90 percent cover. Nevertheless, for a whole year, the burned savanna remains a very different environment from the unburned savanna with its more dense and tangled vegetation.

The savanna is burned each year in January, certain zones being protected by firebreaks. In order to study its specific effects upon the fauna, an out–of–season experimental fire was made in April (fire 5). Development of the fauna in these burned and unburned zones was studied for one year after fire 1 (1962), 2(1963), 3(1964), 4(1965), 5(1965), and for 3 months after fire 6(1966).

The effects of fire on pentatomid populations are of two types: direct and immediate, and indirect by long-term transformation of the environment.

FIG. 8. The savanna after the fire. Contrast this with Fig. 7.

STUDY TECHNIQUES

Samples are obtained of the arthropod population from quadrats of 25 m^2 and 100 m^2. Twelve or 24 collectors converge from the perimeters towards the center, pulling up all the vegetation tuft by tuft, and capturing the animals on the soil or in the grass. These are immediately killed, sorted, and then weighed. With the exception of the aerial fauna, most of the large and medium sized arthropods are obtained. (Gillon and Gillon, 1965, 1967).

DIRECT EFFECT OF FIRE ON THE PENTATOMIDS

From the beginning to the end of the fire, certain heliophilous pentatomid species may be seen climbing rapidly up the stalks of the grasses and flying away.

These fugitives make up the greater part of the pentatomids that disappear immediately with passage of the fire, i.e. 92 percent.

The disappearances of flightless nymphs and winged adults are not identical and vary with distance from the beginning of the fire; close to the beginning of the fire there are fewer winged than apterous individuals, in distant areas more winged than apterous individuals are found (Fig. 10, 11, & 12). As has often been seen, the insects

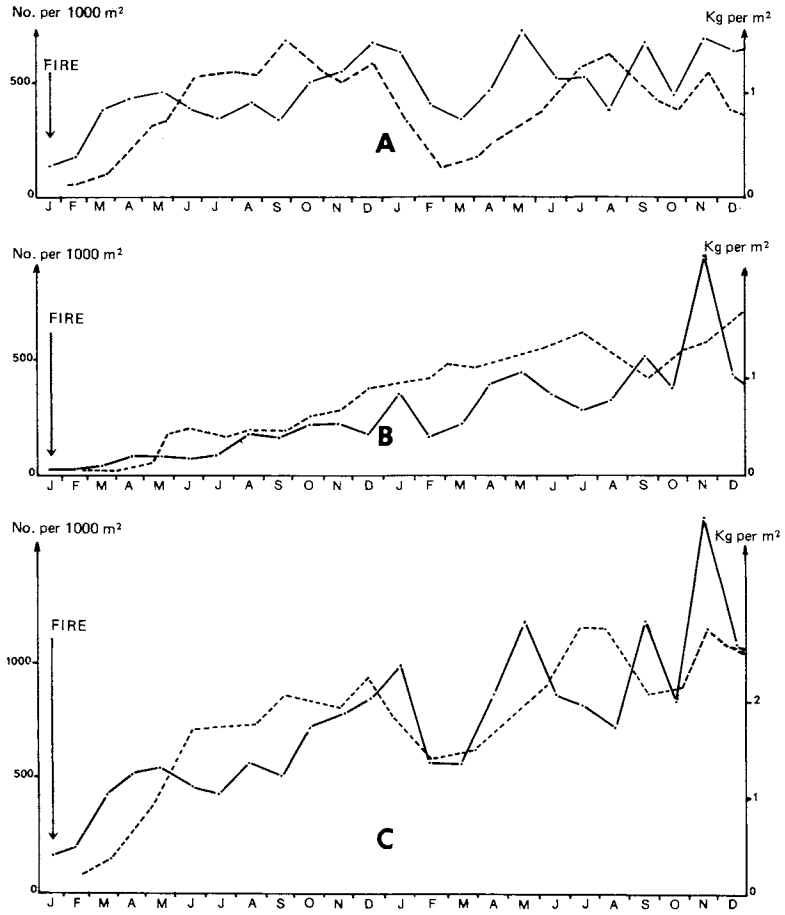


FIG. 9. Monthly development of the level of pentatomids (solid lines) compared to that of the quantity of vegetation (dashed lines) during the year following fire, and the following year, if fire doesn't occur (Roland, 1967). A) development of heliophilous pentatomids compared to that of living vegetation; B) development of sciaphilous pentatomids compared to that of the dead vegetation; C) development of all pentatomids compared to that of the total vegetation.

capable of flight escape up on advance of the fire, and, after the latter has progressed a certain distance, begin to return to the newly burned land.

Among the winged adults, the sciaphilous species are most damaged by the passage of the fire, and consequently the total population is more heliophilous after the fire.

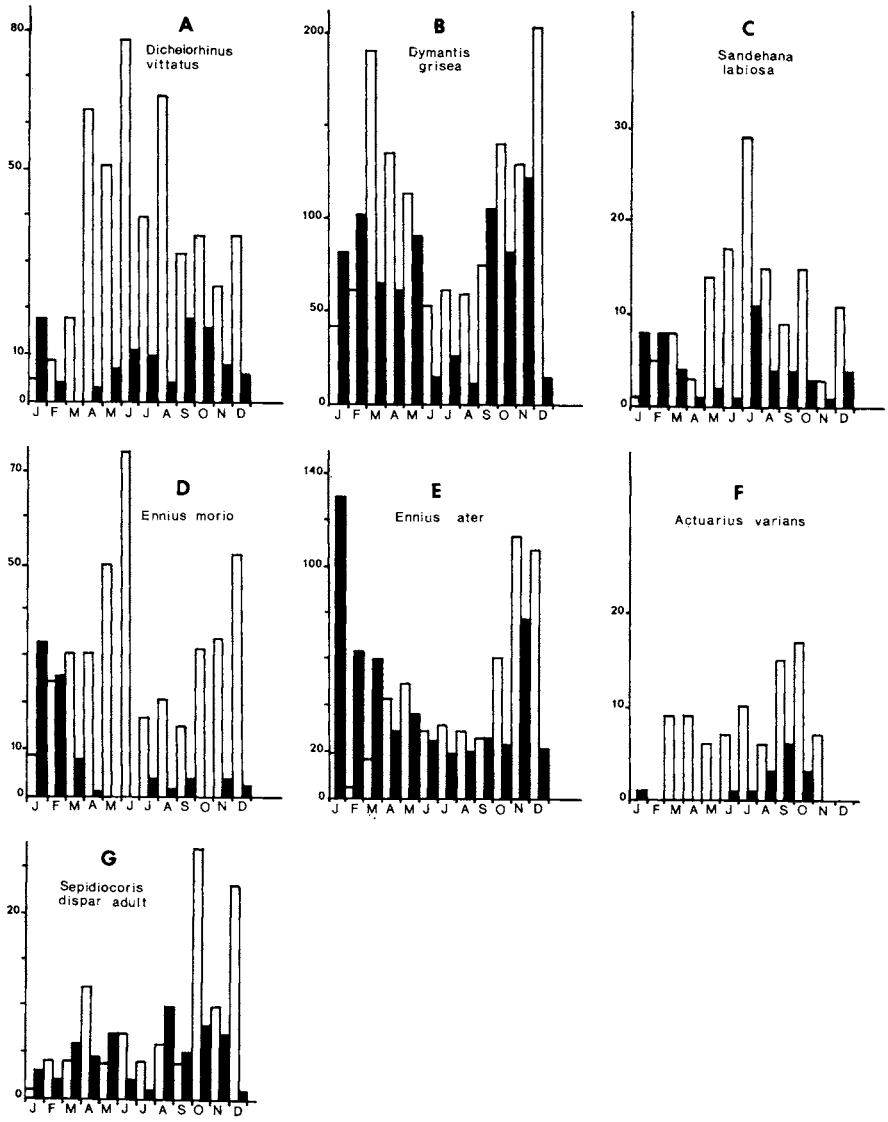


FIG. 10. Comparative monthly development of the level of the main species of pentatomids per 1000 m^2 of burned savanna (open bars) and of unburned (solid bars) during the year.

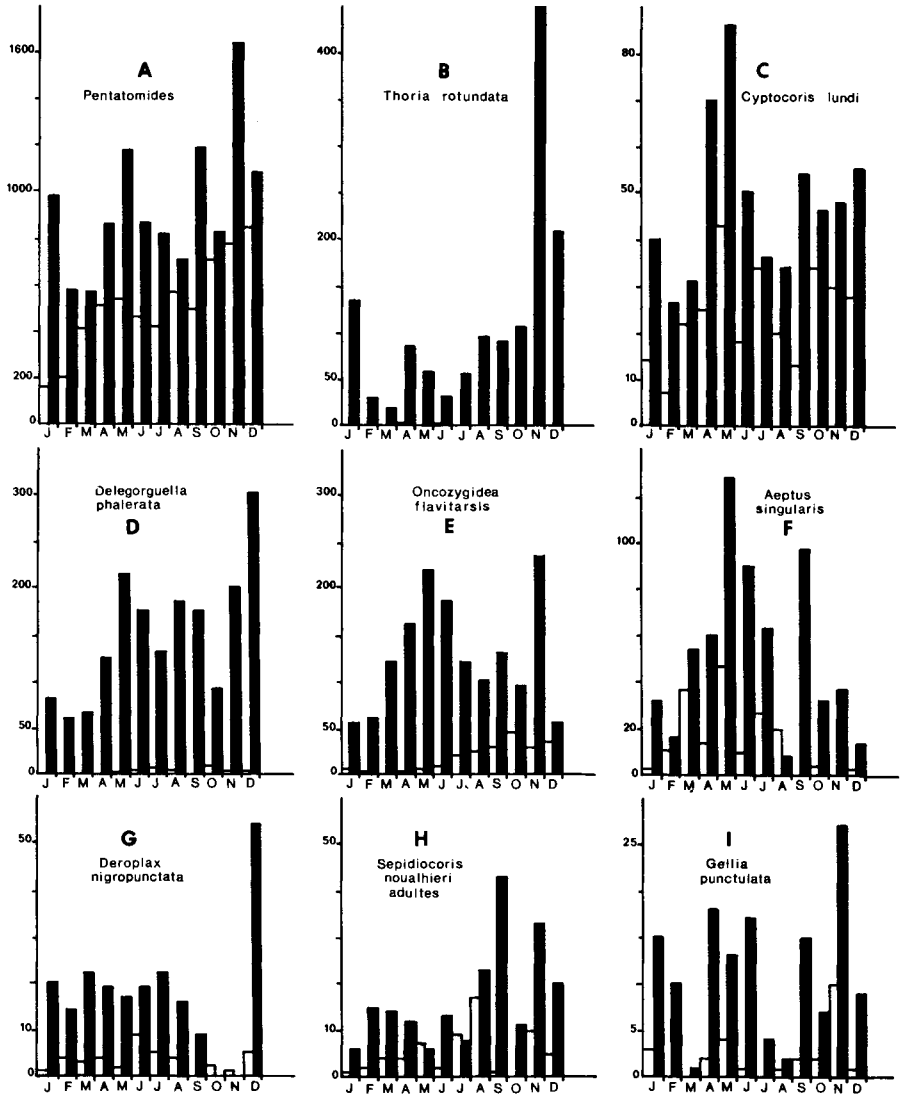


FIG. 11. Comparative monthly development of the level of the main species of pentatomids per 1000 m² of burned savanna (open bars) and of unburned savanna (solid bars) during the year.

Specimens of various species of pentatomids have been found partly charred after the fire: adults and nymphs of *Gellia dilatata*, adults of *Dymantis grisea*, *Aeliomorpha divisa*, *Thoria gillonae*, *Lob-*

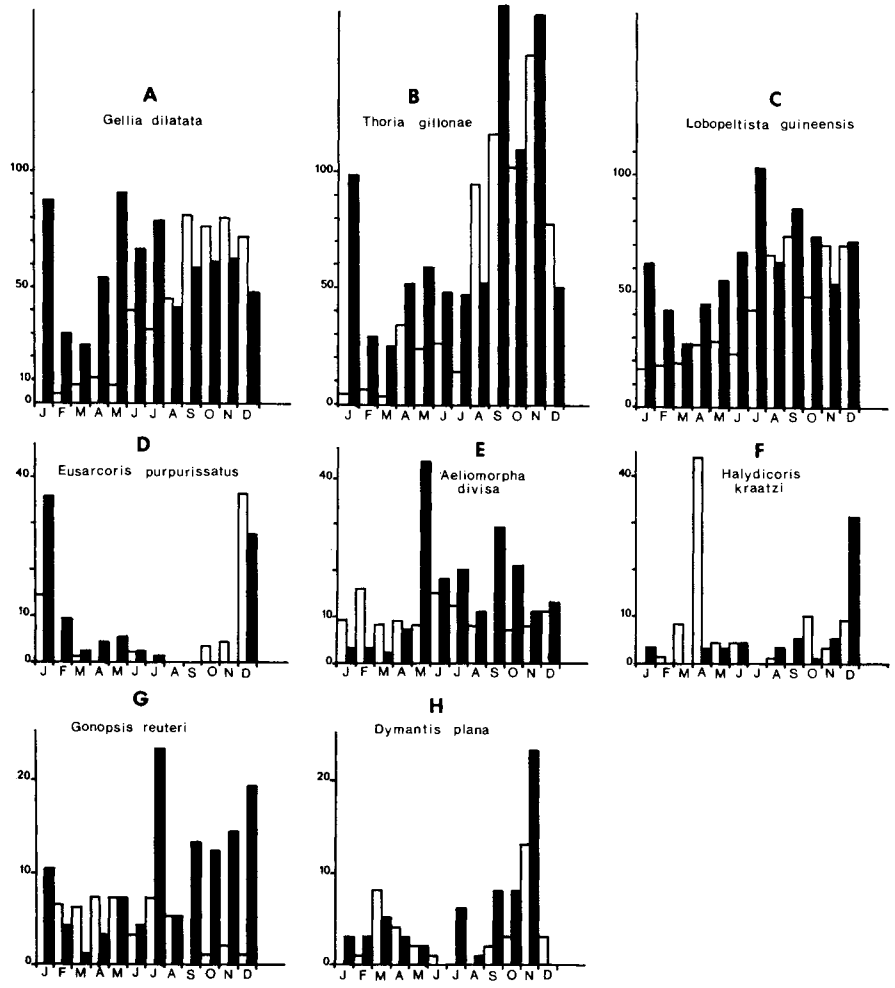


FIG. 12. Comparative monthly development of the level of the main species of pentatomids per 1000 m² of burned savanna (open bars) and of unburned savanna (solid bars) during the year.

opeltista guineensis, and *Cyptocoris lundi*. There are readily flying species such as *Dymantis grisea*, which have been observed flying before the fire, as well as sciaphilous species which are not readily mobile: *Thoria gillonae*, *Cyptocoris lundi*. Apparently, fire can burn all types of pentatomids.

The Effect of the January Fires on the Population in General

In January, before fire, 939 pentatomids inhabited an average of 1000 m^2 of savanna. After fire, there were only 160. Thus, fire causes the disappearance of 83 percent of the population.

The average decrease during the fires is of the same magnitude considering either the total number of pentatomids, or only those which can't fly, or only winged adults (Table 2), indicating that the total population must have responded passively to the fire.

However, during each of the fires, the disappearance of winged and non-winged bugs was not identical. When the effects of fires 2 and 4 were studied in well-burned areas, near the starting line of the fire (at 100 and 200 m), the winged bugs were proportionately fewer than apterous species (Table 2). After fires 3 and 6, studied in regions which were allowed to extinguish themselves, far from their line of departure (500 m and 2 km), there were proportionately more winged than apterous species. These results confirm our observations; at the beginning of fire, insects capable of flying flee before the flames, and after a certain extension of the fire, begin to return to the freshly burned savanna. The heliophiles are burned less frequently than the sciaphiles because the former are better fliers.

Proportionately, more winged sciaphilous adults disappear than do apterous pentatomids. Since there is no reason to believe that winged adults, even sciaphilous ones, are more easily burned than apterous ones, some of these adults must have been able to flee the fire.

Table 2. Number of Pentatomids Per 1000 m^2 of Savanna and Percent Decrease

	January fires[1]					April fire
	2	3	4	6	$\bar{M}$	5
Before fire	998	1230	807	640	939	1000
After fire	80	140	210	227	160	487
% gone: Total	92%	89%	74%	65%	83%	51%
Apterous	79%	93%	67%	76%	84%	27%
Winged adults	95%	86%	76%	60%	83%	63%
Winged sciaphilous adults	97%	91%	83%	100%	90%	59%
Winged heliophilous adults	94%	85%	69%	58%	79%	67%
Distance in km to the starting line of the fire	0.2	0.5	0.1	2.0		0.2

[1] No collection was made before and after fire 1.

Without a single means of protection other than hiding, 16 out of 100 apterous pentatomids still manage to survive the passage of flames. Part of the sciaphilous adults succeeded in fleeing as well as part of the heliophiles; but it must be remembered that they already possess a beneficial reaction to the burned zones since they have the reflex to seek refuge in them during the fire.

Thus, the proportion of heliophiles increases from 68 percent on the eve of the fire to 82 percent after its passage (Table 8).

Examination of stomach contents of kites during the course of the fire, shows that they have no predelection for pentatomids, which must be paltry prey compared to the grasshoppers, locusts, and mantids which also fly from the fire (Gillon and Roy, 1968; Gillon and Pernes, 1968).

The Effect of the April Fire

The late fire is of special interest since it took place after the first big rains when pentatomids start to lay. The savanna was full of young nymphs, 300/1000 m^2 (instead of 183 in January) and had not burned in more than 15 months. Thus, the vegetation was damper, more complex, stratified, and thicker than in January, only 12 months after the previous fire. The population of pentatomids was richer in sciaphilous species, containing only 59 percent heliophiles.

As after fire 2, the effect of the late fire was studied near its line of departure (around 200 m). Its effect on the winged bugs was also more accented than on the apterous ones.

There were 487 pentatomids per 1000 m^2 after the fire, compared to 1000 before, reducing the population by 51 percent, less of an effect than in January.

In an equal area, fewer apterous bugs disappeared than in January, and since the nymphs were much more numerous to begin with, the proportion spared was almost three times higher than during the January fires.

The winged adults were also less affected than in January. The April fire, although strong and fast, apparently disturbed all the pentatomids less, probably because the habitat offered more possibilities for hiding and protection.

As opposed to the January fire, disappearance was small in the

sciaphilous adults, even less than in the heliophiles, probably for the same reasons: the complexity of the habitat before the fire.

In spite of its intensity, the late fire had a less important direct effect on the population of pentatomids than the January fires. It also had little effect on the composition of the population, because the proportion of heliophilous species remained constant at 60 percent (Table 8).

Table 3 shows the concentration and percentage of individual species after each fire.

TABLE 3. NUMBER PER 1000 M² (N) AND PERCENT (%) OF EACH SPECIES BEFORE (A) AND AFTER (B) THE JANUARY FIRES AND THE APRIL FIRE

[1] S = sciaphilous species.
[2] H = heliophilous species.

		January Fires				April Fire			
		N		%		N		%	
		A	B	A	B	A	B	A	B
S[1]	*Cyptocoris lundi*	50	14	5.3	8.8	120	80	12.8	16.5
	Oncozygidea flavitarsis	64	6	6.8	3.8	134	13	13.4	2.7
	Thoria rotundata	17	0	1.8	0.0	107	67	10.7	13.8
	Thoria gillonae	138	5	14.7	3.1	33	0	3.3	0.0
	Deroplax nigropunctata	29	1	3.1	0.6	7	20	0.7	4.1
	Dichelorhinus vittatus	25	5	2.7	3.1	—	—	—	—
	Gellia dilatata	84	0	8.9	0.0	13	33	1.3	6.8
	Gellia punctulata	16	3	1.7	1.9	60	0	6.0	0.0
	Lobopeltista guineensis	53	15	5.6	9.4	27	0	2.7	0.0
	Aeptus singularis	33	3	3.5	1.9	27	60	2.7	12.4
H[2]	*Dymantis grisea*	112	42	11.9	26.3	33	13	3.3	2.7
	Delegorguella phalerata	19	3	2.0	1.9	366	186	36.6	38.4
	Ennius ater	145	20	15.4	12.5	20	0	2.0	0.0
	Ennius morio	41	9	4.4	5.6	—	—	—	—
	Aeliomorpha divisa	50	14	5.3	8.8	7	0	0.7	0.0

DEVELOPMENT OF THE POPULATION DURING THE MONTH FOLLOWING FIRE

AFTER THE JANUARY FIRES

Even if regrowth of plants is rapid, recovery is only about 40 percent at the end of 1 month; the grasses are only about 10 cm high, and the plant biomass is only 50 g per 100 m². In one month, the population increased from 160 to 195 pentatomids per 100 m². In the course of this month, the population increased principally in species of sun-dwellers, and their proportion increased from 82–87 percent (Table 8). On the contrary, most of the shade-seeking ani-

TABLE 4. RELATIONSHIP BETWEEN THE DIRECT EFFECT OF FIRE AND THE DEVELOPMENT OF THE POPULATION AS A WHOLE DURING THE FOLLOWING MONTH

	Fire 2	Fire 3	Fire 4	Fire 6	Fire 5
Decrease the day of fire	92%	89%	74%	64%	51%
Remaining the day after fire	8%	11%	26%	36%	49%
Collected one month after fire	25%	17%	22%	11%	25%

mals disappeared from the burned savanna. Table 6 shows by species, their occurrence 1 month after the fires.

The greater the initial loss, the more rapid is the recolonization of the new habitat and conversely (Table 4). In fact, the population actually continued to decrease after fires with a relatively small initial pentatomid loss (4 and 6). Thus, there is a sort of compensatory equilibrium.

Nymphs, small in number after the fires, decreased further since they become adults in 1 month, but do not yet lay eggs themselves (Table 5).

In contrast to what occurred after all the other January fires where recolonization started after the fires, there was flight from the zone burned by fire 6 by heliophilous pentatomids. This flight, particular to 1966, can be explained by the unique presence that year of a contiguous zone burned 10 months previous (after the late fire 5), thus having the characteristics of a burned savanna in which the plant cover had already been reconstructed. This contiguous zone attracted the heliophilous pentatomids more than areas recently denuded by fire.

TABLE 5. DEVELOPMENT OF THE POPULATION PER 1000 M² OF SAVANNA FROM THE DAY AFTER THE FIRE UNTIL THE FOLLOWING MONTH

		January fires					April fire
		2	3	4	6	$\overline{M}$	5
Nymphs	After fire	6	23	53	40	32	207
	1 month after	18	0	25	0	10	67
Adults	After fire	74	117	157	187	128	280
	1 month after	229	206	157	67	185	186
Sciaphilous adults	After fire	40	7	47	0	24	140
	1 month after	47	16	31	7	26	7
Heliophilous adults	After fire	34	110	110	187	104	140
	1 month after	182	190	126	60	159	179
Percent heliophilous	After fire	50	93	73	100	82	60
Pentatomids	1 month after	76	92	83	90	87	97

TABLE 6. VARIATIONS OF THE LEVEL PER 1000 M² OF THE PRINCIPAL SPECIES FROM THE DAY AFTER THE FIRE (B) UNTIL THE FOLLOWING MONTH (C) AFTER FIRES 2, 3, 4, 5, AND AFTER FIRE 6

	Fires 2, 3, 4, 5		Fire 6	
	B	C	B	C
Cyptocoris lundi	27	7	—	—
Oncozygidea flavitarsis	9	2	—	—
Thoria rotundata	11	0	—	—
Sepidiocoris noualhieri adults	3	2	—	—
Delegorguella phalerata	34	0	13	—
Ennius ater	17	5	20	—
Gellia dilatata	11	4	—	7
Deroplax nigropunctata	4	4	—	—
Aeptus singularis	13	16	—	—
Thoria gillonae	5	7	—	—
Dichelorhinus vittatus	2	14	20	—
Gonopsis reuteri	0	6	—	—
Lobopeltista guineensis	5	17	60	20
Sandehana labiosa	1	5	—	—
Dymantis grisea	48	72	7	7
Ennius morio	6	24	20	7

Table 6 shows the levels of the various species during this time.

Two 100 m² collections made 1 month after fire 1, one in burned savanna, and the other in a humid depression which did not burn, in the middle of the same area, show the exchanges which took place between these two habitats during this time (Table 7). Certain species show a clear preference for the burned habitat over this depression, but most of them concentrate in this small, unburned area.

TABLE 7. COMPARISON OF TWO COLLECTIONS OF 100 M², MADE ONE MONTH AFTER FIRE, ONE NEXT TO THE OTHER, ONE IN BURNED SAVANNA (SB) AND THE OTHER IN A UNBURNED DEPRESSION (SNB) IN THE MIDDLE OF THE BURNED SAVANNA

	SB	SNB
Dymantis grisea	3	—
Sandehana labiosa	2	—
Dichelorhinus vittatus	3	—
Oncozygidea flavitarsis	1	29
Sepidiocoris noualhieri	2	4
Thoria gillonae	2	1
Aeptus singularis	1	2
Delegorguella phalerata	—	9
Ennius ater	—	13
Ennius morio	—	8
Gellia dilatata	2	5
Gonopsis reuteri	—	2
Lobopeltista guineensis	—	24
Deroplax nigropunctata	—	2
TOTAL (all species)	16	102

After the Late Fire 5

We have seen that the effect of this fire is unique. It was not very destructive, so, as after the less destructive January fires, there is a diminution in the population during the month following the fire (Table 4). Of the large numbers of nymphs which withstood the fire, two-thirds disappeared in the following month (Table 5), probably many dying, for being young, they did not have time to become adults. In addition, the eggs sticking to the grass leaves are particularly vulnerable to fire, and were all burned the day of the fire. For 1 or 2 weeks following, the absence of vegetation or support for the eggs must have interrupted egg laying and could account for the decrease in number of young at this time.

The adults also diminish in number. The sciaphiles, especially numerous after the fire, desert the new habitat completely (Table 5). The sun-lovers, by contrast, had a tendency to recolonize the new habitat, and the population again takes on the characteristics of a burned savanna where the sun-lovers represent the large majority (97 percent) of the population as after the January fires. (Table 8).

THE POPULATION TWO MONTHS AFTER FIRE

After the January Fire

The big rains release vigorous regrowth and at the same time, egg-laying of the pentatomids. Vegetative biomass increased ten-fold in one month, to 500 g of green herbs per m^2. There were also 412 pentatomids per 1000 m^2, representing a clear increase in density over the previous month. This was partly because the pentatomids had begun to lay (nymphs increased from 10 to 1000/m^2), and also because the density of adults doubled, as recolonization continued, still mainly by heliophilic species, whose proportion, in one month, increased from 87–91 percent partly due to reproduction. The density of the shade-dwelling species remained relatively constant.

If the results of the collections at more than 100 m from unburned savanna are separated from those at less than 100 m, one obtains very different densities: 143 adults and 73 nymphs per 1000 m^2 far from the unburned savanna against 353 and 108 near these limits, thus

twice as many. This indicates that recolonization of the burned habitat is made from the unburned zones where insects appear to hide the day of fire. There is also more specific variety near the unburned zones (Table 10).

After the Late Fire.

The effects of the late fire on the savanna were similar to that of the January fires (Table 8): augmentation of the general density,

Table 8. Development of the Population on 1000 m² of Savanna from the Eve of the Fire (A), the Day After Fire (B), One Month After (C), Two Months After (D) until Three Months After (E) in Savanna Burned in January and in April

January Fires	A	B	C	D	E
Total	939	160	195	412	509
Nymphs	183	32	10	101	201
Adults	756	128	185	311	308
Sciaphilous adults	239	24	26	37	78
Heliophilous adults	517	104	159	274	230
Percent heliophiles (nymphs and adults)	68%	82%	87%	91%	84%
April Fire					
Total	1000	487	253	567	413
Nymphs	300	207	67	233	147
Adults	700	280	186	334	266
Sciaphilous adults	347	140	7	33	20
Heliophilous adults	353	140	179	301	246
Percent heliophiles (nymphs and adults)	59%	60%	97%	93%	92%

massive eclosions of nymphs, recolonization of the new habitat by sun-loving adults. One notices that 2 months after the late fire (in June), the proportion of nymphs attained 41 percent, whereas it was only 25 percent in March, 2 months after the January fires. This difference is explained by the more advanced stage of the population at this time, most of the females being mature, and having already had time to lay by the April fire.

THE POPULATION THREE MONTHS AFTER THE FIRE

After the January Fire

In the month of April, there are an average of 509 pentatomids per 1000 m². The increase over the preceding month (Table 8) is due only to the increase in the number of nymphs, which doubled

to 201 per 1000 m². Recolonization of the burned habitats by the adults seemed to lessen.

Collections made in areas close to the unburned savanna were no longer richer than the others, especially with respect to adults. Thus, the population of pentatomids stabilized in the burned savanna, and the species found the habitat favorable for reproduction.

Since the shade-lovers also started to reproduce, the proportion of sciaphilous to heliophilous species approached equilibrium; the heliophilous species now represent 84 percent of the population (Table 8).

After the Late Fire

No new adults emerged and the population became temporarily impoverished in adults (Table 8). In general, the months of July and August are periods when the total population passes through a minimum (Fig. 11A).

All species reproducing at this time show that they found the habitat which suits them in the burned savanna, and that their presence is

Table 9. Development of the Density on 1000 m² of the Principal Species from the Eve of Fire (A), the Day After Fire (B), One Month After (C), Two Months After (D) and Three Months After (E) the Fires of January and that of April

[1] S = sciaphilous species.
[2] H = heliophilous species.

		January Fires					April Fire				
		A	B	C	D	E	A	B	C	D	E
S[1]	*Cyptocoris lundi*	50	14	7	22	25	120	80	—	14	13
	Oncozygidea flavitarsis	64	6	2	—	2	134	13	—	7	—
	Thoria rotundata	17	—	—	—	2	107	67	—	—	2
	Thoria gillonae	138	5	7	4	34	33	—	—	—	20
	Sepidiocoris noualhieri ad.	1	1	2	4	4	7	13	—	—	—
	Sepidiocoris disper adults	5	1	4	4	12	—	—	—	—	—
	Deroplax nigropunctata	29	1	4	3	4	7	20	7	—	4
	Delegorguella phalerata	19	3	—	—	—	366	186	—	—	—
H[2]	*Dichelorhinus vittatus*	25	5	9	18	63	—	—	40	147	106
	Gonopsis reuteri	5	—	6	6	7	13	—	—	—	—
	Gellia dilatata	84	—	4	8	11	13	33	—	20	47
	Gellia punctulata	16	3	—	—	2	60	—	—	—	—
	Lobopeltista guineensis	53	15	17	18	26	27	—	20	46	34
	Sandehana labiosa	9	1	5	8	3	—	—	—	—	—
	Aeptus singularis	33	3	11	37	14	27	60	40	13	—
	Dymantis grisea	112	42	61	190	135	33	13	100	220	93
	Ennius ater	145	20	5	17	43	20	—	—	—	7
	Ennius morio	41	9	25	31	31	—	—	—	20	34
	Halydicoris kraatzi	3	—	1	8	44	—	—	—	12	—

not linked by chance to the dilution of individuals on the available areas. Their return to the burned savanna is an active movement.

If the number of adults remained the same from one month to another, it was not necessarily a sign of population stability. There were two major changes: two sciaphilous species gradually recolonized the burned savanna (*Thoria gillonae* and *Sepidiocoris dispar*) (Table 9). To compensate, there was a lowering in the density among certain sun-lovers such as *Dymantis grisea*, which had been among the first to lay eggs in the burned savanna, and whose adults, parents of the first generation, began to disappear.

CHANGES IN THE POPULATION IN THE ABSENCE OF FIRE

During this time, the populations in areas which did not burn develop and respond to the repercussions of fire.

From January to Feburary

In the absence of fire, the overall density of pentatomids decreases from January to February, partly as a consequence of the time in the life cycle when the oldest nymphs of the last generation of the year become adults, but mainly as a consequence of the disappearance of a large number of adults, both heliophilous and sciaphilous (Table 11). This month is the dryest in the savanna, and the time when there is most chance of fire, if it were not voluntarily set before. Thus, fire would occur at the most favorable time for the pentatomids.

During the dry season Pollet (1970) observed a clear increase in the density of pentatomids along the edge of the forest gallery, even before fire, showing that part of the population hid in these more humid and favorable habitats. This explains in part the general reduction in population in unburned savanna.

However, all species aren't affected equally by this general lowering in population, and some even become more abundant (e.g. *Delegorguella phalerata*, *Dymantis grisea*, and *Sepidiocoris noualhieri*) (Table 13). The population is being transformed into a more heliophilic type by the disappearance of the sciaphiles (Table 11)

which are more sensitive to changes in climate and probably also those which have the greatest tendancy to hide in the humid regions.

It would be expected that the population along the edge of unburned savanna next to burned savanna would be richer in all the pentatomids having fled the fire and burned savanna, thus richer in sciaphilous species and poorer in heliophilous species. In fact, quite the contrary happens. Near the burned savanna:

1) The overall density of pentatomids is lower than in open unburned savanna (Table 12).

2) The density of sciaphilous species is lower.

3) The density of the heliophilous species is slightly elevated.

4) With the exception of *Lobopeltista guineensis*, all the heliophilous species which start to recolonize the burned savanna in February are less abundant near the burned savanna than far from it. By contrast, heliophilous species which are more abundant near the burned savanna than far from it are the same species which recolonize the burned habitats the following month (Table 13).

TABLE 10. DENSITY PER 1000 M² OF THE PRINCIPAL SPECIES AT MORE THAN 100 M FROM THE UNBURNED SAVANNA, AND AT LESS THAN 100M.

[1] S = sciaphilous species.

[2] H = heliophilous species.

		More than 100 m. from SNB	Less than 100 m. from SNB
S[1]	*Cyptocoris lundi*	6	26
	Thoria gillonae	6	4
	Sepidiocoris noualhieri	—	5
	Sepidiocoris dispar	—	5
	Deroplax nigropunctata	3	3
H[2]	*Dichelorhinus vittatus*	37	13
	Gonopsis reuteri	3	6
	Gellia dilatata	—	10
	Lobopeltista guineensis	12	20
	Sandehana labiosa	—	10
	Aeptus singularis	—	47
	Dymantis grisea	110	211
	Ennius ater	12	18
	Ennius morio	18	34
	Halydicoris kraatzi	6	9
	TOTAL (all species)	216	461

FROM FEBRUARY TO MARCH

The general density of pentatomids increases slightly because the nymphs of the first generation begin to appear. The number of

sciaphilous species augments considerably while that of the heliophilous species remains stationary (Table 11). Since the density of pentatomids decrease along the length of the forest-galleries (Pollet, 1970) and thus probably also in all the refuge zones, it can be assumed that the population as a whole spread everywhere in the savanna. The first big rains gave the habitat the humidity favorable to the regrowth of vegetation and a biotype propitious to the sciaphilous pentatomids. Thus the population becomes more sciaphilous and the proportion of heliophiles falls to 60 percent.

Comparing the population situated near the burned savanna to that in the middle of the unburned savanna, the following conclusions can be drawn (Table 12):

1) The total populations of both are equally abundant.

2) The former increases in sciaphilous pentatomids in the same proportion as the rest of the unburned savanna, but still remains poorer.

3) The former increases in heliophilous pentatomids, whereas the rest of the unburned savanna loses them.

In March, the edge zone of unburned savanna once again shows a population of an intermediary type between those of the two adjacent habitats. However, the number of heliophilous species is increasing, and thus it is diverging from the rest of the unburned savanna.

This edge is also a transition zone between the two habitats at the specific level (Table 13). In the sciaphilous species in general, density follows an increasing gradient from the burned savanna to the middle of the unburned. By contrast, it decreases for most of the heliophilous species.

Also in March, a gradient in the distribution of species was observed showing progressive recolonization of the burned zones from the unburned savanna.

TABLE 11. DEVELOPMENT OF THE POPULATION ON 1000 M² IN UNBURNED SAVANNA FROM JANUARY UNTIL APRIL

	J	F	M	A
Adults	756	506	580	598
Nymphs	183	15	39	312
Total	939	521	619	910
Number of sciaphiles	305	151	246	392
Number of heliophiles	634	370	373	518
Percent heliophiles	68%	71%	60%	57%

FROM MARCH UNTIL APRIL

As in burned savanna, the density of pentatomid nymphs increases (Table 11). This is the middle of their reproductive period. The proportion of heliophilous species decreases a little, again due to the more important increases in the number of sciaphilous species.

Near burned savanna, the population is again less dense than further away, but still presents an intermediate type between that of the two habitats. Still, the differences between the edge zone and the middle zone of the unburned savanna continue to lessen the equilibrating of the heliophilous and sciaphilous species (Table 12). The edge of the unburned savanna seems to be emptying itself of heliophilous species, for they are less numerous than in the rest of the unburned savanna. Their density is approaching that of the burned savanna.

In general, all species increase in the unburned savanna except *Ennius ater* and *E. morio* which plainly disappear, and *Dymantis grisea* which loses relative importance. *Oncozygidea flavitarsis* and *Delegorguella phalerata* become the dominant species in the unburned habitats (Table 13).

TABLE 12. COMPARATIVE DEVELOPMENT OF THE POPULATION ON 1000 M² OF BURNED SAVANNA (SB) AND OF UNBURNED SAVANNA NEXT TO BURNED SAVANNA (SNB X) AND FAR FROM BURNED SAVANNA (SNB Y) IN FEBRUARY, MARCH AND APRIL

		F		M		A	
		N	%	N	%	N	%
Sciaphiles	SB	26	13%	37	9%	83	16%
	SNB X	117	24%	191	30%	270	39%
	SNB Y	188	34%	307	51%	565	44%
Heliophiles	SB	169	87%	372	91%	426	84%
	SNB X	373	76%	444	70%	427	61%
	SNB Y	367	66%	293	49%	710	56%
Total	SB	195		409		509	
	SNB X	491		635		697	
	SNB Y	555		600		1275	

BALANCE SHEET AT THE END OF THREE MONTHS

Because the burned savanna has achieved a certain stability, it is possible to balance the phenomena linked directly to the passage of fire and its immediate repercussions.

During the first 3 months after the fire, the population of penta-

tomids undergoes profound changes. In the burned savanna, 80 percent of the population disappears, and the habitat is completely transformed, resulting in a new, temporarily smaller population which is different from that of the pre-fire savanna.

In the absence of fire, the population structure does not remain fixed because of the existence of burned areas close by, attracting certain species and excluding others, and because of the succession of the habitat. It is difficult to imagine what would happen to the population in the total absence of fire. The heliophilous species would not be able to leave the habitat invaded by the vegetation to colonize open areas. Would they be gradually eliminated in the covered habitat where the sciaphilous species predominate?

Recolonization of the burns is first by the most mobile heliophilous species, followed by the sciaphiles. At the end of 3 months the proportion of heliophiles is still 84 percent, whereas it was only 68 percent before the fires.

In the unburned areas, the population becomes more sciaphilous in character than before the fires, although *Delegorguella phalerata*, a heliophile, become dominant in these habitats.

Since the heliophilous species reproduce first, the population cycle of the burned savanna appears precocious: in March 25 percent of the population is already composed of nymphs, whereas in unburned savanna, the first wave of nymphs appears in April.

During the 3 months following fire, the population of pentatomids shows a gradient between a heliophilous type in the burned savanna, toward a more sciaphilous type in the unburned. The edge of the unburned savanna is intermediate in character.

One can not explain the predominance of heliophiles on the edge of the unburned savanna by insects hiding from the fire, because the sciaphilous species would also be more abundant on the edge than in the rest of the unburned savanna. In addition, collections were all made upwind from the fire. The gradient evokes a picture of progressive movement of the heliophiles from well within the unburned savanna towards the middle of the burned savanna. These species accumulate near the burned savanna in February, then begin to pass into it in March, and finally, propogate in all parts of the burned savanna in April. Conversely, the sciaphilous species leave the

TABLE 13. DEVELOPMENT OF THE AVERAGE DENSITY PER 1000 M² OF THE PRINCIPAL SPECIES OF PENTATOMIDS FROM JANUARY UNTIL APRIL IN UNBURNED SAVANNA, AND FOR EACH MONTH THE DENSITY AT LESS THAN 50 METERS FROM THE BURNED SAVANNA (X) AND AT MORE THAN 50 METERS (Y)

[1] S = sciaphilous species.
[2] H = heliophilous species.

		J	F	M	A	F X	F Y	M X	M Y	A X	A Y
S[1]	*Cyptocoris lundi*	50	22	38	75	20	25	37	39	66	100
	Oncozygidea flavitarsis	64	63	131	174	46	82	89	177	90	267
	Thoria rotundata	17	3	12	50	4	2	17	7	57	60
	Thoria gillonae	138	32	26	55	25	40	11	42	17	91
	Sepidiocoris noualhieri	2	15	10	10	8	23	6	15	7	15
	Sepidiocoris dispar	5	3	3	5	4	2	—	7	—	9
	Deroplax nigropunctata	29	12	26	23	9	15	31	22	33	24
	Delegorguella phalerata	19	29	71	149	20	38	94	47	90	222
	Dichelorhinus vittatus	25	4	—	1	3	5	—	—	3	—
	Gonopsis reuteri	5	4	2	4	1	8	2	2	—	7
	Gellia dilatata	84	26	27	71	34	18	31	23	80	85
	Gellia punctulata	16	4	1	20	8	—	2	—	3	34
H[2]	*Lobopeltista guineensis*	53	37	29	58	41	31	43	13	17	96
	Sandehana labiosa	9	9	6	—	7	12	6	5	—	—
	Aeptus singularis	33	18	55	74	22	12	56	53	130	64
	Dymantis grisea	112	124	83	79	120	128	94	71	66	107
	Ennius ater	145	49	62	25	71	23	74	50	13	38
	Ennius morio	41	30	10	1	17	45	5	17	—	2
	Aeliomorpha divisa	5	4	2	3	8	—	—	3	—	5

unburned savanna, demonstrating the influence of the burned savanna beyond its borders. It is difficult to say how far, since, unfortunately, the farthest collections were only 250 m from burned savanna.

It is possible to think of a physical and climatic field going beyond the borders of the bare and blackened burned savanna which must store heat much more intensively (up to 50 C after Monnier). In addition, the earth undergoes a strong evaporation and creates extreme climatic conditions, very different from the vegetated zones. Within certain limits, the climate in the neighborhood of the burned savanna is hotter and drier, with greater fluctuations. This climatic gradient induces the displacement of pentatomids in opposite directions.

The repercussions of the late fire are more pronounced. As has been shown, in the absence of fire, the population continues to develop towards a more sciaphilous type until the fire in April, and thus its transformation is even more drastic. Even though different at the beginning, the consequences of fire are similar in all cases, and a

population identical to that which appeared after the January fire is reconstituted, showing how strong the influence of the new habitat is. This can be seen in *Oncozygidea flavitarsis*, *Thoria rotundata*, *Gellia punctulata*, *Aeptus singularis*, and especially *Delegorguella phalerata*, all of which are excluded from the new habitat.

The same species as after the January fire recolonize the newly burned savanna after the late fire.

DEVELOPMENT OF THE POPULATION UNTIL THE NEXT FIRE

The Population as a Whole

Pentatomids in burned savanna always remain less abundant than in unburned. In a yearly total, there are about one half as many pentatomids in burned savanna, even considering the relatively stable populations from the beginning of May (Table 14). This difference is constant, and the two populations grow in parallel during the year (Fig. 11A).

The number of heliophiles remains slightly less in the burned savanna, but this difference tends to diminish with time, since they increase only in the burned zones. In contrast, even if the sciaphiles increase in the burned savanna, they still remain only 30 percent of those in the unburned savanna where their density continually increases.

Thus the population of pentatomids is limited by recurrent fires, and in the absence of fire, its size doubles.

Thus the burned savanna seems to be an impoverished habitat. Each year, whether fire occurs or not, the development of the vegetal floor offers the same possibilities to the sun-lovers: the layer of living erect herbaceous species produced during the year (Fig. 9A). The handicap represented to the heliophiles by the direct action of fire and the disappearance of the herbal layer may be sufficient to explain the small difference in their density in burned and unburned savanna, a difference which tends to disappear at the end of the year.

The overall population of pentatomids increases proportionately to the total weight and complexity of the vegetation (Fig. 9C). In par-

TABLE 14. COMPARATIVE DEVELOPMENT OF THE POPULATION IN BURNED SAVANNA (SB) AND IN UNBURNED SAVANNA ON 1000 M² (SNB)

	J[1]	F[1]	M[1]	A[1]	M	J	J	A	S	O	N	D	Total
SB													
Total	160	195	412	509	539	458	422	568	502	714	778	845	6102
Nymphs	32	10	101	201	185	158	151	214	206	336	331	242	2167
Adults	128	185	311	308	354	300	271	354	296	378	447	603	3945
Sciaphiles	28	26	37	83	86	76	90	172	164	219	231	178	1390
Heliophiles	132	169	375	426	453	382	332	396	338	495	547	667	4712
Percent heliophiles	82%	87%	91%	84%	84%	83%	79%	70%	67%	69%	70%	79%	77%
SNB													
Total	984	569	569	860	1176	866	819	713	1186	830	1637	1077	11286
Nymphs	195	22	34	277	364	245	298	267	426	332	697	415	3572
Adults	789	547	535	583	812	621	521	446	760	498	940	662	7714
Sciaphiles	360	173	234	398	452	352	292	335	521	392	954	445	4908
Heliophiles	624	396	335	462	724	514	527	378	665	438	683	632	6378
Percent heliophiles	63%	70%	59%	54%	62%	59%	64%	53%	56%	53%	42%	59%	57%

[1] Populations of the first four months in SNB are not the same as in Table 11, because populations in savanna which has not burned for one year are mixed with those of savanna which has not burned for two and three years, to show up the differences between populations of burned and unburned savanna.

ticular, the accumulation of dead vegetation offers a whole range of varied habitats that are covered and protected from climatic fluctuations and that are favorable to the sciaphilous species (Fig. 9B).

COMPARISON OF THE SPECIFIC COMPOSITION OF THE POPULATION IN THE BURNED AND UNBURNED SAVANNA.

During the entire year, burned and unburned habitats are always present. Their spread and their surfaces vary according to the years and the climatic conditions occurring the day of the fire. Our intervention only determines their geographical limits.

Thus, the insects always exercise a choice between the two changing habitats. Certain species have a clear preference for one or the other of the habitats.

Dichelorhinus vitattus, Dymantis grisea, Sandehana labiosa, Ennius ater, E. morio, Actuarius varians, and *Sepidiocoris dispar* prefer the burned savanna the year-round (Fig. 10).

Thoria rotundata, Cyptocoris lundi, Delegorguella phalerata, Oncozygidea flavitarsis, Aeptus singularis, Deroplax nigropunctata, Sepidiocoris noualhieri, and *Gellia punctulata* prefer the unburned savanna (Fig. 11).

Certain species return to the burned savanna only after the influence of fire on the habitat is attenuated: *Gellia dilatata, Thoria gillonae, Lobopeltista guineensis, Eusarcoris purpurissatus* (Fig. 12A, B, C, D).

Others return to the burned savanna just after the fire, but as the differences between the two habitats lessen, they redistribute themselves, or even select unburned savanna: *Aeliomorpha divisa, Halydicoris kraatzi, Gonopsis reuteri, Dymantis plana* (Fig. 12E, F, G, H). This phenomenon is exemplified by *Halydicoris kraatzi*, for example, which is attracted to burned savanna after fire by a composite, *Vernonia guineensis*, which grows and flourishes during the first few months after fire. When this plant lignifies and dries out, *Halydicoris kraaztzi* leaves it and spreads itself over several different plant species (Duviard, 1970).

The species are spread out in the two habitats (Table 15 and Fig. 13). It is possible that certain species would be less abundant in burned savanna than unburned, but their proportion might be greater,

TABLE 15. LEVELS AND PERCENTAGES OF THE MAIN SPECIES OF PENTATOMIDS DURING THE WHOLE YEAR IN BURNED SAVANNA (SB) AND IN UNBURNED SAVANNA (SNB) (1000 M² PER MONTH)

	Levels		Percentages	
	SB	SNB	SB	SNB
Dymantis grisea	1258	773	20.6%	6.8%
Thoria gillonae	659	905	10.8%	8.0%
Ennius ater	530	529	8.7%	4.7%
Lobopeltista guineensis	489	736	8.0%	6.5%
Dichelorhinus vittatus	459	105	7.5%	0.9%
Gellia dilatata	457	700	7.5%	6.2%
Ennius morio	391	84	6.4%	0.7%
Cyptocoris lundi	288	576	4.7%	5.1%
Oncozygides flavitarsis	202	1523	3.3%	13.5%
Aeptus singularis	176	630	2.9%	5.6%
Sandehana labiosa	130	51	2.1%	0.5%
Sepidiocoris dispar	124	71	2.0%	0.6%
Aeliomorpha divisa	111	181	1.8%	1.6%
Cyclopelta funebris	104	12	1.7%	0.1%
Actuarius varians	86	15	1.4%	0.1%
Halydicoris kraatzi	84	58	1.4%	0.5%
Sepidiocoris noualhieri	73	258	1.2%	2.3%
Deroplax nigropunctata	40	212	0.7%	1.9%
Delegorguella phalerata	27	1809	0.4%	16.0%
Thoria rotundata	4	1368	0.1%	12.1%

showing that the burned savanna attracted a particular species more than other species. Thus, *Thoria gillonae*, *Ennius ater*, *Lobopeltista guineensis*, and *Gellia dilatata* show a clear preference to the burned savanna. (Table 15).

STAGES IN THE DEVELOPMENT OF THE POPULATION.

Even if burned and unburned habitats coexist, they are really the same habitats at different stages of succession. After fire, the habitat goes back to zero and develops until the next fire. Without fire, succession continues toward greater complexity. The population which inhabits these savannas also develops and its composition varies as a function of the age of the habitat. The day of the fire, all species are affected. One month after, *Dichelorhinus vittatus* and *Gonopsis reuteri* regain the burned zones. Two months after, in March, *Dymantis grisea*, *Sandehana labiosa*, *Ennius morio*, *Actuarius varians*, *Halydicoris kraatzi*, and *Dymantis plana* colonize the burned savanna. In April, it is *Ennius ater's* turn, in August, *Gellia dilatata*, *Thoria gillonae*, and *Lobopeltista guineenis*, in October, that of *Eusacoris purpurissatus*.

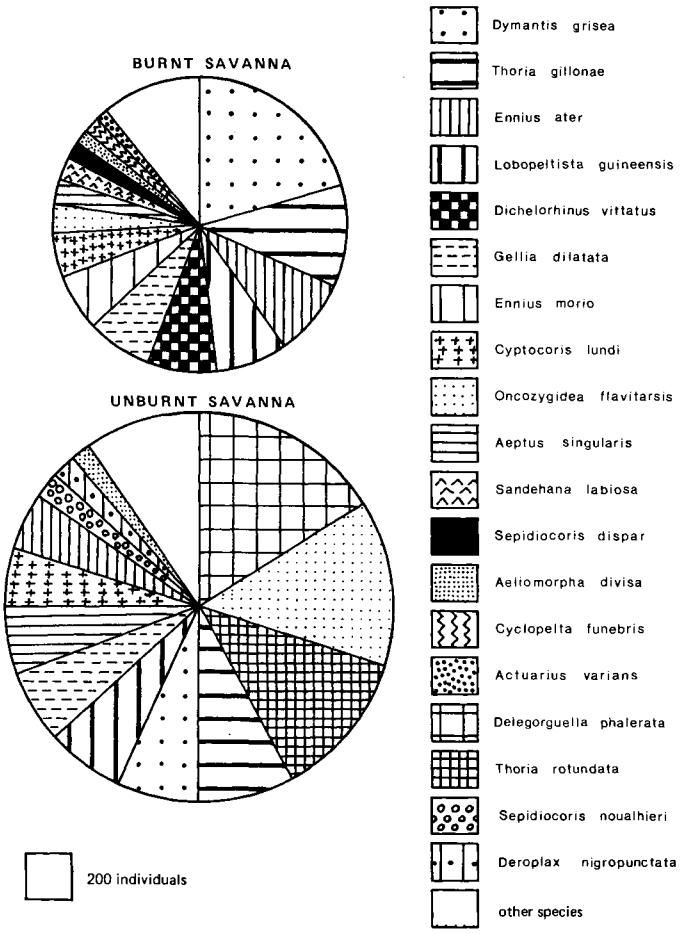


FIG. 13. Specific composition of the pentatomid population in burned savanna and in unburned savanna during the whole year (after Table 15).

One year afterwards, if fire does not re-occur, certain species begin to dominate the population: *Thoria rotundata, Delegorguella phalerota.*

SPECIES DOMINATING THE POPULATION

In savanna burned during the year, one species, *Dymantis grisea*, clearly dominates the others and represents more than 20 percent of

the annual population (Table 15), twice as abundant as any other species. *Dymantis grisea* and *Thoria gillonae,* second in order of importance in burned savanna are also among the most common in unburned savanna where they are fourth and fifth in order, respectively.

In unburned savanna, three species are dominant, and almost equivalent: *Delegorguella phalerata*, *Oncozygidea flavitarsis*, and *Thoria rotundata* (Table 15). The first two are extremely rare in burned savanna. *Oncozygidea flavitarsis* is ninth in order of importance in burned savanna.

The most successful species in burned savanna are the most ubiquitous in the savanna generally, thus the most adaptable. Those which succeed in unburned savanna do not develop in the burned savanna, perhaps not finding the proper conditions.

In the unburned savanna, three of the seven predominant species are sciaphilous, while of the seven most abundant species in the burned savanna, only one, *Thoria gillonae,* is sciaphilous, since the burned savanna offers less oportunity for sciaphiles.

Two less important species, however, find conditions clearly favorable in burned savanna since they are four times more abundant than in unburned: *Ennius morio* and *Dichelorhinus vittatus.*

TABLE 16. DEVELOPMENT OF THE POPULATION OF THE SAVANNA BURNED IN APRIL, 1965 FOR ONE YEAR AFTER FIRE (150 m^2 PER MONTH)

	A	M	J	J	A	S	O	N	D	J	F	M
Thoria rotundata	10	—	—	—	—	—	—	—	—	—	—	2
Cyptocoris lundi	12	—	2	2	—	—	—	—	3	2	1	1
Delegorguella phalerata	28	—	—	—	—	—	—	—	3	5	3	10
Deroplax nigropunctata	3	1	—	—	—	—	—	—	3	—	—	—
Sepidiocoris noualhieri	2	—	—	—	—	—	—	—	1	—	—	2
Gellia punctulata	—	—	—	—	1	—	2	—	—	—	—	—
Oncozygidea flavitarsis	2	—	1	—	1	—	1	—	2	5	8	12
Aeptus singularis	9	6	2	—	—	—	7	4	1	1	2	8
Dichelorhinus vittatus	—	6	22	16	12	2	6	6	19	3	1	—
Dymantis grisea	2	15	33	14	18	1	24	42	28	8	5	19
Sandehana labiosa	—	—	—	—	7	—	—	3	2	3	—	—
Actuarius varians	—	2	—	5	5	2	3	4	2	—	—	—
Ennius morio	—	—	3	5	2	4	13	22	6	6	2	6
Ennius ater	—	—	—	1	3	2	7	7	8	5	1	3
Gellia dilatata	5	—	3	7	2	6	7	6	12	3	1	2
Thoria gillonae	2	—	1	—	1	—	1	—	2	5	8	12
Lobopeltista guineensis	—	3	7	5	1	11	10	21	4	13	13	10
Eusarcoris purpurissatus	—	—	—	—	—	—	—	—	14	8	—	—
Aeliomorpha divisa	—	4	7	2	1	—	—	—	1	—	—	—
Halydicoris kraatzi	—	—	2	—	—	2	8	7	9	—	—	—

Two additional species, *Delegorguella phalerata* and *Thoria rotundata* enter into competition with the two dominant ones, and limit their importance when burned savanna is not burned again the following year. *Delegorguella phalerata,* a heliophilous species, takes the place of *Dymantis grisea* and *Thoria rotundata,* a sciaphilous species, takes that of *Thoria gillonae.* There is room for still another sciaphilous species already present (but only ninth in rank), *Oncozygidea flavitarsis,* which is given new opportunities by the accumulation of dead herbs. The two previously dominant species of burned savanna, *Dymantis grisea* and *Thoria gillonae* are thus pushed back to the third or fourth position in the absence of fire.

The survival of two species characteristic of unburned savanna, *Delegorguella phalerata* and *Thoria rotundata,* hinges on the existence each year on zones which don't burn.

LONG TERM EFFECTS OF THE LATE FIRE

It has been stated that the direct effect of the late fire on the population was weak since it spared mainly sciaphilous and other species characteristic of unburned savanna. It was not until the following month that the population presented a facies characteristic of burned savanna. Because of the ephemeral characters it would present, no count was made the day after the April fire.

Comparing the population of the savanna burned in April (SBA) with that burned in January of the same year (SBJ) and the unburned zones of this year (SNB), from the month of May until the following December, it can be seen that whatever the date of the fire, the number of pentatomids remains small compared to that in the unburned savanna during the same period (Table 17).

The reconstitution of the population is more rapid in April since the fire occurs later in their life-cycle, and the adults reproduce beginning with their return to the burned savanna. The reconstitution of the vegetation is also more rapid after the late fires (Monnier, 1968).

There are also more pentatomids in SBA than in SBJ because of the greater numbers of heliophilous species which more than compensate for any lack of sciaphiles (Table 17).

TABLE 17. COMPARISON OF THE POPULATION FROM JUNE UNTIL DECEMBER 1965 IN THE SAVANNA BURNED IN JANUARY (SBJ), IN APRIL (SBA) AND IN UNBURNED SAVANNA (SNB). (150 M² PER MONTH)

	SBJ	SBA	SNB
Thoria rotundata	—	—	124
Cyptocoris lundi	5	7	78
Delegorguella phalerata	10	3	320
Deroplax nigropunctata	5	4	9
Sepidiocoris noualhieri adults	2	1	5
Gellia punctulata	—	3	47
Oncozygidea flavitarsis	24	5	255
Aeptus singularis	2	20	143
Dichelorhinus vittatus	48	89	1
Dymantis grisea	63	175	67
Sandehana labiosa	5	12	2
Actuarius varians	9	23	2
Ennius morio	60	55	2
Ennius ater	41	28	58
Gellia dilatata	78	43	93
Thoria gillonae	26	18	81
Lobopeltista guineensis	73	62	139
Eusarcoris purpurissatus	27	14	8
Aeliomorpha divisa	13	15	52
Halydicoris kraatzi	9	28	27
Sciaphiles	70	37	561
Heliophiles	484	625	1075
% Heliophiles	87%	94%	66%
TOTAL (all species)	554	662	1636

The specific composition of the population which is collecting in SBA is very close to SBJ with several exceptions (Table 17):

Species normally characteristic of unburned savanna (Fig. 11) are similar in SBA to that of SBJ, and much less abundant than in the unburned savanna. The level of *Oncozygidea flavitarsis* is especially weak in SBA which can be explained by its habit of not returning to burned areas until 6 months after the January fires (Fig. 11E). The opposite can be observed in *Aeptus singularis* (Fig. 11F).

Species which recolonize burned areas precociously (Fig. 10) are more abundant in SBA than in SNB, but also more so than in SBJ due to their strong and selective preference for the more recently burned areas (Fig. 10 A,B,C,F). Only *Ennius morio* is not more abundant in SBA. *E. ater*, the last of the precocious species to colonize the January burns (Fig. 10E) is even less abundant than in SBJ. *Halydicoris kraatzi* which occurs in large numbers from the first months after the January fire (Fig. 12F) is much more abundant in SBA than in SBJ which is too old to attract them.

The habitats burned in April only begin to attract species in De-

cember which had recolonized the January burns several months after fire (Table 16). Their density thus remains lower in SBA than in SBJ.

The population which forms in SBA is thus generally of the burned type with the difference that it is younger than that of SBJ during the same period; it is thus richer in heliophiles and poorer in sciaphiles.

If development of the population of SBA is followed beyond the month of December by protecting it artificially from the dry season fires up until the following March (11 months after fire), species reappear which recolonize burned areas late (Table 16). Also, a phenomenon amplified by the passage of fire in neighboring zones occurs, the appearance of species characteristic of unburned savanna. At the same time, heliophilous species leave this zone for those which have just burned.

Whatever the date of the fire, it always has the same effect on the habitat, and by indirect effect, on the population of pentatomids. The type of population at the time of fire varies only according to the age of the habitat. The more aged the population, the more it will have to change to return to its starting point. If fire occurs before the first big rains, thus before the beginning of the reproductive season of the pentatomids, the population will have an entire year to reconstitute itself. If fire occurs after the beginning of the reproductive period, the population will reconstitute itself more quickly, but will not have sufficient time to complete its development, and certain species late to recolonize burned habitats will not have time to regain burned areas if fires occur as usual in the following dry season.

DEVELOPMENT OF THE STRUCTURE OF THE POPULATIONS

Only the 19 principal species of pentatomids, constituting 90 percent of the population (Table 1) will be considered.

Spearmann's coefficient of rank correlation was calculated between two populations by comparing the relative importance of each species (their respective ranks in the midst the population) according to the

method already described (Gillon and Pernes, 1968). The coefficient of correlation thus numbers from −1 to +1 the degree of similarity between the two populations. The population of each month is thus compared with each of all the other months in both habitats, thus with 23 other populations (Table 18). Then a dendrograph was constructed linking two by two the most similar populations, and the total of the burned and unburned populations by calculating the arithmetic average of their respective coefficients (Sokal and Sneath, 1963).

One concludes that (Fig 14):

1) The whole year, populations which have undergone fire are very different from those which haven't, and the general level of similarity between these two types of populations is very low, beyond the level of probability 0.05. Thus, fire plays a dominant role in the structure of the populations.

2) The similarity between the different monthly populations is greater in the unburned savanna than in the burned, thus fire introduces a certain heterogeneity.

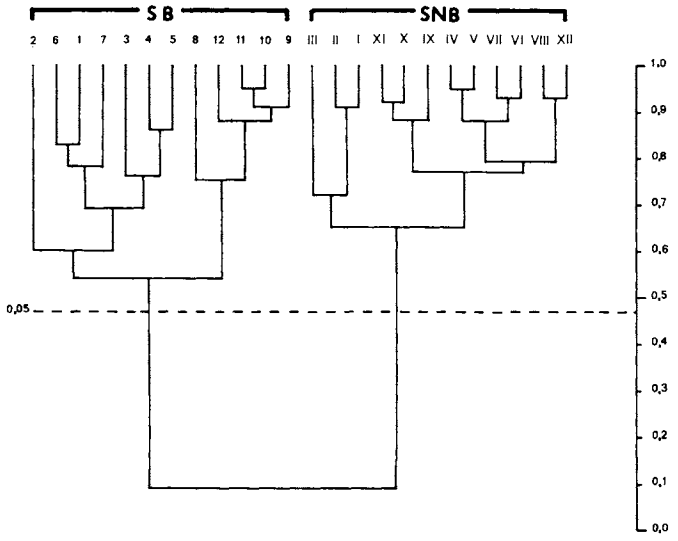


FIG. 14. Dendrograph of the relationship between the population of each month in burned and unburned savanna during the year.

3) In the absence of fire, the cycle of the seasons molds the structure of the populations. In the dry season, from January to March, the populations are more similar between themselves and different from the rest taken as a whole. The populations from April to July, first rainy season, are distinct from those of September to November, second rainy season. The populations of August and December, two periods of climatic transition, are similar to each other.

4) If fire occurs, there are two main types of populations:

One type is the population of the second rainy season from August to December. The populations of these months are very similar to each other.

The second type (from January to July) is not very homogeneous. This is the time when the populations of the dry season, very disturbed by the recent occurrence of fire, hardly resemble each other. The population, little changed in its structure right after the January fire, has a fairly large degree of resemblance with those of the following months. In contrast, the population of February, 1 month after fire, is very different from the others, but still resembles more the populations of the first months after fire than the latter are similar to those of the last months of the year. The influence of fire on the structure of the population is less important than the influence of seasonal development or the age of the habitat since the last fire. From March, the population reconstitutes itself and is fairly similar to the following months.

5) The strongest coefficients of correlation link the populations of succeeding months, except those of August and December in the unburned savanna, which are among the most similar to each other.

6) The strongest dissimilarities are manifested by negative coefficients of correlation between the populations from January to August in burned savanna, and those of April to December in unburned savanna (Table 18). There is thus a development of the population's structure which becomes more and more different from what it was after the fire as it becomes further removed from fire in time.

Two principles dominate the evolution of the structure of the populations: Fire disturbs the population less profoundly by its direct action than by changing the habitat.

TABLE 18. COEFFICIENTS OF RANK CORRELATION OF SPEARMANN BETWEEN THE POPULATION OF EACH MONTH IN BURNED SAVANNA (1 TO 12) AND IN UNBURNED SAVANNA (I TO XII) WITH EACH OF THE 23 OTHERS

	1	2	3	4	5	6	7	8	9	10	11	12	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1	1.00	0.65	0.62	0.68	0.69	0.83	0.79	0.51	0.55	0.61	0.68	0.77	0.44	0.37	0.22	0.01	0.07	0.10	0.01	0.11	0.01	0.02	0.08	0.12
2		1.00	0.56	0.56	0.52	0.60	0.69	0.49	0.35	0.38	0.37	0.49	0.10	0.00	0.08	0.00	0.16	0.00	0.11	0.13	0.14	0.09	0.08	0.09
3			1.00	0.77	0.76	0.72	0.74	0.35	0.40	0.46	0.49	0.49	0.20	0.12	0.12	0.11	0.06	0.20	0.22	0.38	0.10	0.16	0.16	0.32
4				1.00	0.83	0.82	0.66	0.76	0.62	0.65	0.70	0.77	0.33	0.16	0.02	0.17	0.15	0.22	0.25	0.27	0.04	0.00	0.02	0.26
5					1.00	0.68	0.63	0.65	0.40	0.41	0.44	0.59	0.14	0.03	0.05	0.29	0.43	0.34	0.38	0.54	0.24	0.22	0.22	0.51
6						1.00	0.78	0.64	0.73	0.73	0.79	0.83	0.39	0.25	0.03	0.10	0.06	0.18	0.11	0.16	0.05	0.01	0.03	0.19
7							1.00	0.60	0.68	0.73	0.66	0.70	0.41	0.36	0.28	0.16	0.23	0.12	0.16	0.00	0.13	0.18	0.13	0.32
8								1.00	0.78	0.75	0.69	0.80	0.27	0.18	0.00	0.10	0.03	0.01	0.03	0.04	0.10	0.22	0.11	0.16
9									1.00	0.93	0.89	0.82	0.51	0.41	0.17	0.11	0.13	0.09	0.13	0.17	0.23	0.38	0.30	0.01
10										1.00	0.95	0.89	0.56	0.55	0.35	0.22	0.25	0.19	0.20	0.27	0.35	0.45	0.42	0.09
11											1.00	0.92	0.57	0.53	0.29	0.15	0.16	0.09	0.13	0.21	0.24	0.36	0.35	0.08
12												1.00	0.56	0.52	0.29	0.08	0.12	0.04	0.08	0.10	0.16	0.25	0.29	0.01
I													1.00	0.91	0.64	0.67	0.58	0.46	0.60	0.58	0.60	0.69	0.77	0.55
II														1.00	0.80	0.74	0.67	0.57	0.67	0.68	0.67	0.69	0.88	0.61
III															1.00	0.80	0.79	0.70	0.72	0.61	0.69	0.53	0.62	0.60
IV																1.00	0.95	0.85	0.89	0.82	0.86	0.82	0.83	0.81
V																	1.00	0.87	0.91	0.73	0.78	0.78	0.77	0.68
VI																		1.00	0.93	0.83	0.80	0.71	0.69	0.79
VII																			1.00	0.86	0.84	0.76	0.73	0.83
VIII																				1.00	0.80	0.82	0.84	0.93
IX																					1.00	0.91	0.86	0.69
X																						1.00	0.92	0.68
XI																							1.00	0.69
XII																								1.00

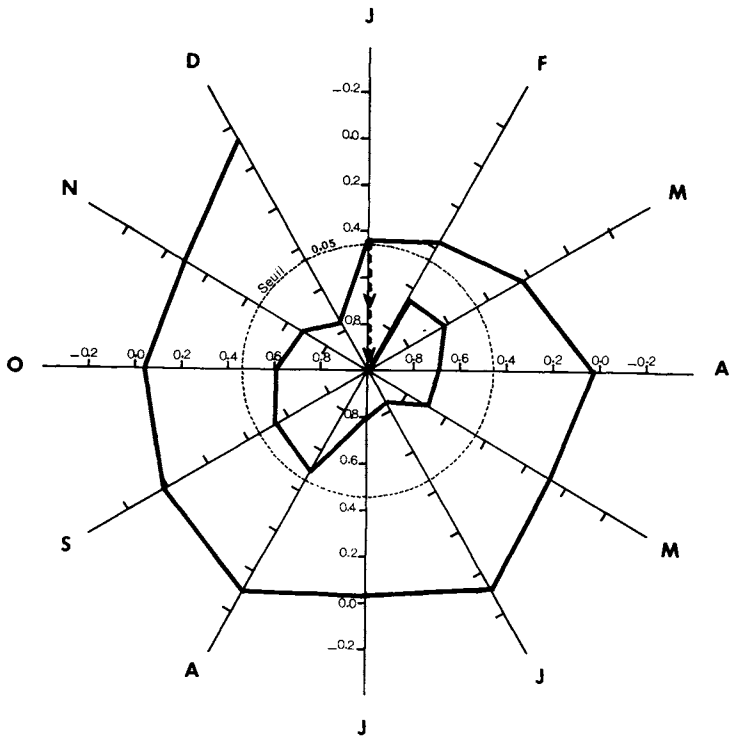


FIG. 15. Development of Spearmann's coefficient of correlation between the population of January after the fire, and that of each of the other months, without further intervention of fire.

Fire affects the population for 1 year or until the following fire. Starting with point zero representing the state of the population the day after the fire, the structure of the population evolves continually (Fig. 15). During 1 year after fire, the structure of the population remains fairly homogeneous, rhythmed only by the seasons. At the installation of the dry season, in November and December, the structure of the population becomes close even to that of January after the preceding fire. The population seems adapted to the annual passage of fire, and the species keep about the same rank in the midst of the population for the whole year. If fire occurs, the population comes again to point zero. In the absence of fire, the population develops naturally towards a very different type.

CONCLUSIONS

The conclusions of this study are not readily generalised to other types of savanna. The fact that the savanna never burns in its entirety each year, and never the same day, maintains a richer and more varied population.

A certain number of species are probably present only because of the existence each year of unburned zones, e.g. *Delegorguella phalerata* and *Thoria rotundata* disappear almost entirely from the burned zones each year.

Even the abundance of certain species in the burned savanna seems equally linked to the spared zones, those which hide in unburned zones in large numbers during one part of the year, waiting for the burned areas to reach a certain maturity so they can reproduce (e. g. *Gellia dilatata*, *Lobopeltista guineensis*, *Thoria gillonae*).

If the savanna burned entirely each year, logically the population should become impoverished in sciaphilous species, since they could recover only by reproduction of the low levels of survivors.

We have seen that if the population of pentatomids can accomplish an entire annual cycle after the passage of fire, it has time to become complex and rich before the next fire. Normally in this region fire is most probable in the dry season: December, January or February. Out-of-season fires which affect the population late in the year and prevent its complete development before the following dry-season fire are rare and localized and usually deliberately set. Their impoverishing effect on the species diversity is zero.

Fire is not a very destructive factor. It simplifies the habitat which thus maintains a population of pentatomids of heliophilous type. Certain authors (e.g., Adjanohoun, 1964) believe that fire maintains the savanna, and in its absence the savanna would evolve towards a wooded savanna and then a forest. However, in natural conditions, if fire does not occur in several successive years, the habitat changes indeed, but its chances of burning increase since the quantity of combustible material increases each year. It is only at the beginning of a certain stage in its succession that ligneous species are able to develop and thereby reduce the likelihood of fire. When this happens, the population of pentatomids continues to change, and that

of the unburned savanna of this study is one of the first steps. At the limit of development, the heliophilous species tend to disappear at the same time as fire diminishes in probability. The population then becomes an exclusively sciaphilous type linked to the sub-forest area.

The absence of fire appears to liberate the population to develop towards a different type. Because of this, fire seems to be necessary for the equilibrium of the pentatomid population so that it will remain similar from year to year. Fire cannot be excluded from this habitat without gravely disturbing this equilibrium which has been established for several hundreds of years.

Thus, one can see how much the natural equilibrium of a group of animals can depend on factors in the habitat, and how a modification in only one is sufficient to upset it.

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