

The Effect of Bush Fire on the Principal Acridid Species of an Ivory Coast Savanna

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WHATEVER the various hypotheses on the origin of the Guinean savanna, it is agreed that in modern times, savanna and fire are interdependent. Thus a study of the effects of fire in the savanna risks being merely a description of observable and measurable phenomena, since all, by being there, depend on bush fire. Therefore, it is necessary to dissociate the effects of fire from those changes due only to the periodicity of the seasons. Since these cannot be separated by merely analyzing the "normal" burned savanna, a comparison could be made with zones protected from fire. However, even in the protected zones, fire is not absent, just less recent. To what degree then, does the comparison justify itself?

Generally the savanna burns at the beginning of the calendar year, at the time of maximum dryness. However, since the herbaceous areas are broken by forest galleries which usually stop fires, the countryside is divided into zones which burn at different dates.

Each year, parcels which we will call "unburned" are isolated from the surrounding burned areas for a period of time. During the first years, the accumulation of dried herbs favors fire, but the later appearance of ligneous species makes fire less likely. Finally, climax forest vegetation takes over. Thus, for about 10 years, there is a correlation between the time since the preceding fire and the probability of another. Such a homeostatic tendency favors the maintenance of savanna, but not the work of researchers trying to protect experimental plots from fire.

Each dry season fire reduces the herbage to ashes and marks the beginning of a succession which lasts until the next fire (usually about 1 year). Certain zones might be spared for more than 1 year. In any given area, the periodicity of fire is usually annual with occasional breaks in the cycle, sometimes for several consecutive years.

The unburned zones must not be considered as a reference habitat, but as areas in which succession has not been stopped by the next fire, i.e. an advanced stage of the succession which every parcel undergoes from the moment fire passes. The interest of such zones resides not only in their role as a temporary reservoir of fauna (well known by local hunters), but also as a point of comparison with the rest of the normally burned savanna, since both are a single entity at two stages of succession. This is more than a theoretical comparison, since it corresponds to a real choice for the more mobile animals in the savanna. To this progressive transformation of the savanna into forest, is added the cyclical development linked to the seasons. In the absence of fire the rate of transformation of the savanna is rapid in the beginning, but slows down as the forest climax is approached.

During the first year after fire, the cyclical and continual developments are not distinguishable without a comparison of the burned and unburned zones of the savanna.

Among the arthropods of the preforest savanna of Lamto in the Ivory Coast, D. Gillon and J. Pernes (1968) have shown that grasshoppers are particularly sensitive to the passage of fire. However, fire is a neglected factor in most studies of acridids (Dempster, 1963). We report here the immediate and long term effects of fire on these

insects using data collected during the course of six different fires on the following dates: XII-30-61, I-30-63, I-13-64, I-18-65, IV-7-65 and I-13-66. Qualitative observations of additional fires were also made.

The quantitative collections are made in squares of 25 or 100 m² according to D. Gillon, et al. (1970). Comparison of monthly results combined over several years, between the savanna burned in the dry season and unburned zones (no fire for at least 1 year, but less than 4) will illustrate the effects on the grasshopper population.

MONTHLY COMPARISON OF THE POPULATIONS

The most abundant species comprising together at least 90 percent of the captured animals in both the burned and unburned zones were used. In three cases we have had to combine in the same category two species of the same genus whose young are difficult to distinguish: *Tristria discoidalis* (Fig. 1) and *Tristria marginicosta*, *Acorypha johnstoni* and *Acorypha karschi*, and finally *Orthochtha bisulcata* and *Orthochtha nigricornis*. Fortunately, within each "generic couple" the reactions towards fire seem similar. The species and groups of species used are ranked in decreasing importance relative to the total numbers of acridids captured (Table 1).

In the burned savanna almost twice as many species make up 90 percent of the population as in the unburned savanna.

A two-by-two comparison, with the aide of Spearman's coefficient of rank correlation of the monthly rank for these species, permits us to construct a dendrogram of similarity of months from the point of view of abundance of the species studied (Table 2, Fig. 2). Knowing that the annual cycle of grasshoppers is extremely marked (Y. Gillon and D. Gillon, 1967), one can expect superimposition of the action of fire with that of the season. Figure 2 shows a rather regular succession in the population of the burned savanna, and a more disturbed development in the unburned zones, although the central months of the wet season, April to September, were regrouped into a uniform aggregate clearly in contra-distinction to the dry months of the burned savanna.



FIG. 1. *Tristria discoidalis*, female. This species is abundant only in areas protected from fire for more than one year. See also Fig. 12.

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TABLE 1. THE MOST FREQUENTLY CAPTURED NYMPHS AND ADULT ACRIDIDS IN THE LAMTO SAVANNA, PRESENTED FOR BURNED AND UNBURNED HABITATS IN THEIR ORDER OF ABUNDANCE

In burned savanna (24,859 acridids on 16,425 m ²)			
Species	Caught	%	Cumulative %
<i>Dnopherula obscura</i>	4,564	18.4	18.4
<i>Orthochtha brachycnemis</i>	3,744	15.1	33.4
<i>Machaeridia bilineata</i>	3,288	13.2	46.6
<i>Dnopherula bifoveolata</i>	2,184	8.8	55.4
<i>Tristria</i> spp.	1,485	6.0	61.4
<i>Azarea lloydi</i>	886	3.6	65.0
<i>Coryphosima brevicornis</i>	855	3.4	68.4
<i>Orthochtha</i> spp.	813	3.3	71.7
<i>Catantopsilus taeniolatus</i>	792	3.2	74.9
<i>Acorypha</i> spp.	774	3.1	78.0
<i>Chloroxyrrhepes virescens</i>	590	2.4	80.4
<i>Anablepia granulata</i>	525	2.1	82.5
<i>Tylotropidius didymus</i>	507	2.0	84.5
<i>Mesopsis laticornis</i>	464	1.9	86.4
<i>Rhabdoplea munda</i>	384	1.5	87.9
<i>Brachycrotaphus buttneri</i>	372	1.5	89.4
<i>Chromotruzalis liberta</i>	265	1.1	90.5
In unburned savanna (21,348 on 14,375 m ²)			
<i>Tristria</i> spp.	7,586	35.5	35.5
<i>Rhabdoplea munda</i>	3,563	16.7	52.2
<i>Orthochtha brachycnemis</i>	2,788	13.1	65.3
<i>Dnopherula obscura</i>	2,330	10.9	76.2
<i>Machaeridia bilineata</i>	1,011	4.7	80.9
<i>Coryphosima brevicornis</i>	690	3.2	84.2
<i>Catantopsilus taeniolatus</i>	429	2.0	86.2
<i>Anablepia granulata</i>	346	1.6	87.8
<i>Amphiprosopia adjuncta</i>	291	1.4	89.2
<i>Gelastorhinus africanus</i>	278	1.3	90.5

In the unburned zones an interruption between the months of March and April was observed. This might be explained by the sudden appearance of two species that were particularly abundant in these zones: *Amphiprosopia adjuncta* and *Gelastorhinus africanus*.

Comparison for the same months of the coefficients of rank correlation in the presence and absence of fire revealed a greater similarity between the populations in the dry season than in the wet, which indicated a more important delayed than immediate effect caused by the fire (Fig. 3). In fact, although for the first 3 months differences were slight in the order of the species between the burned savanna and the plots protected from the fire, a sudden change was produced in April, the time at which the dry season adults disappeared and the great majority of the nymphs hatched

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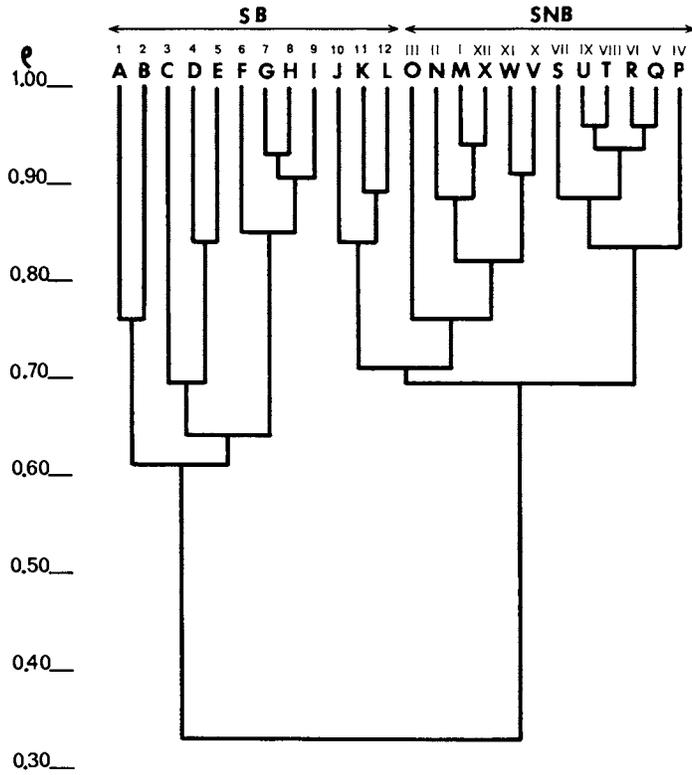


FIG. 2. Dendrograph constructed from the coefficients of correlation from Table 3, uniting and bringing together the different months, in burned and unburned savanna, from the point of view of the order of abundance of the principal acridid species. (ρ = the rank order correlation coefficient.)

out. These differences attenuated gradually up to December when correlation was at its maximum. This was an axis month between the burned and unburned savanna populations. It should be considered the most representative for an overall description of the acridids of this savanna.

Even though a cycle cannot really have a "beginning", the complete change of the habitat brought about by fire is so abrupt and obvious that it seems rather natural to use the population of a recently burned zone as the departure point for the annual succes-

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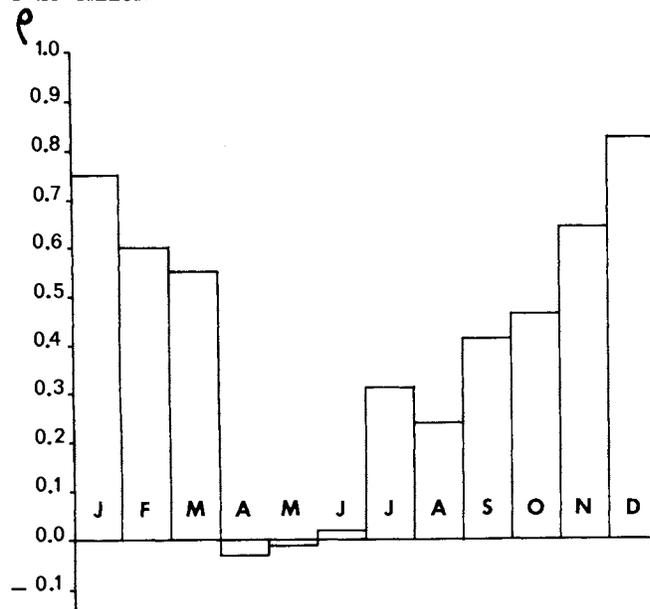


FIG. 3. Month by month comparison of the coefficients of rank correlation between burned and unburned zones (ρ = the rank order correlation coefficient.)

sion. This is the point of view adopted in Fig. 3 where the succession of the savanna is described by the progression of the correlations between the population of January immediately after fire, and that of each other month taken successively from February to December in the burned habitat, then from January to December in the unburned habitat. We thus obtain a picture of this succession, at the same time cyclical and continuous, which we described in the introduction.

Figure 4 shows that the results of the dry season are, as one might now expect, rather similar, even in the unburned zones, to the population of January immediately after fire. The least similar population from this is found at the beginning of the rainy season, in April, both for the burned and unburned zones which are then at their period of maximum dissimilarity.

Guided by the results obtained with the coefficients of correlation, we can undertake an chronological analysis of the events, taking into

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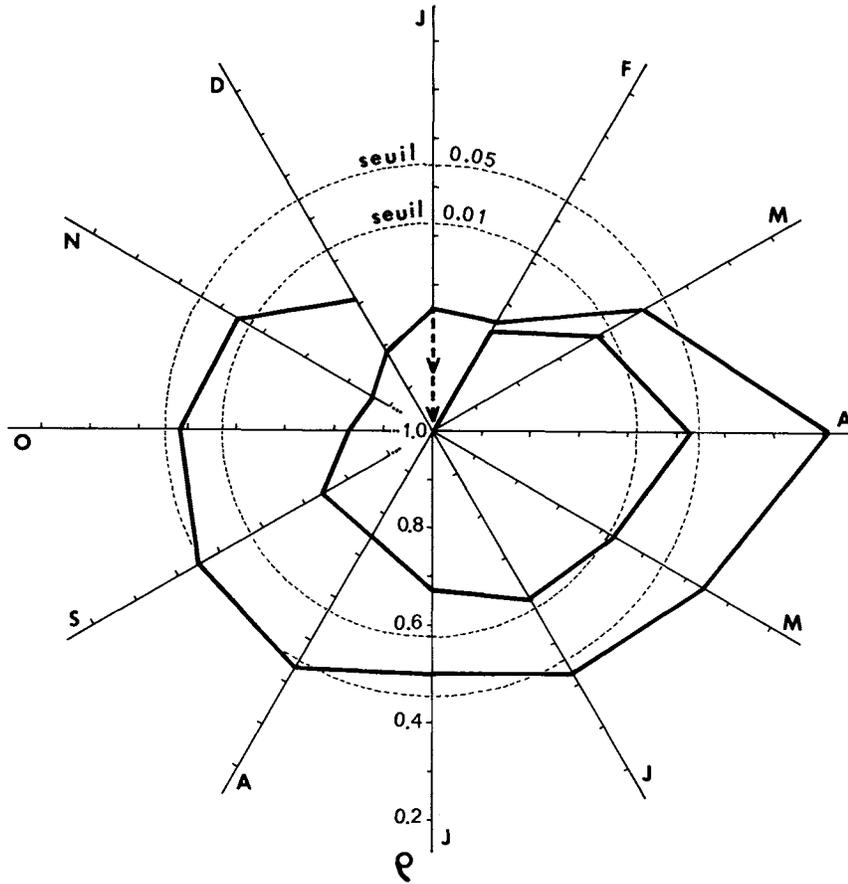


FIG. 4. Development of the coefficient of rank correlation between the population of January right after fire, and that of each of the other months, unburned zones coming after burned zones. (ρ = the rank order correlation coefficient.)

account the densities of the population and of the maximum species possible. Even though the coefficients of correlation only left aside species comprising 10 percent of the population, there are more species in this group than in the group comprising 90 percent of the total numbers. Those species whose behavior with respect to fire is particularly instructive will now be taken into consideration.

ACTION OF FIRE ON THE GRASSHOPPERS

THE POPULATION BEFORE FIRE

The 11 or 12 months since the last fire left the population developing as a function of other parameters such as humidity, nature of the soil and vegetation. It is at this time that the greatest variability may be observed in the specific structure. Pre-fire conditions of 600 square meters were assessed during the month of January 1963, 100 m² January 7, 1964, 400 m² from 15–17 December 1964, and 150 m² 13 January, 1966.

Certain species were found during all 4 years: *Tristria marginicosta*, *Petamella prosternalis*, *Machaeridia bilineata*, *Cannula gracilis*, (Fig. 5) *Rhabdoplea munda*, (Fig 6) *Orthochtha brachyconemis*, *Coryphosima brevicornis*, and *Dnopherula obscura*. Only January 1964 is an exception with its great abundance of *Rhabdoplea munda* (more than half the population), and relative scarcity of *Tanita breviceps*, *Tristria discoidalis*, *Acorypha karschi*, *Tylotropidius didymus*, (Fig. 7) *Azarea lloydi*, *Anablepia granulata*, and *Dnopherula bifoveolata*, present in the other three.

In some species, the adults have disappeared by this time and their eggs have not yet hatched (*Chloroxyrrhepes virescens*, (Fig. 8) *Acroypha johnstoni*, *Amphiprosopia adjuncta*, and *Gelastorhinus africanus*. In *Gymnobothrus linea-alba* we have encountered neither juvenile nor adults in this habitat during this period.

In combining the pre-fire collections, we obtain a slightly artificial picture of the average population, juxtaposing species which are separated during the year by their opposed preferences concerning burning (Table 3). Thus some species of *Tristria* and *Rhabdoplea*, which like places where dead plant matter abounds, are placed next to the Gomphocerinae which disappear almost completely when the savanna doesn't burn for a year such as: *Azarea lloydi*, *Dnopherula bifoveolata*, and *Faureia milanjica*.

Thus the five dominant species do not have a strict preference for burned savanna. They are: *Machaeridia bilineata* (17.6 percent), *Dnopherula obscura* (11.4 percent), *Orthochtha brachycnemis* (10.1 percent), *Catantopsilus taeniolatus* (7.6 percent), and *Coryphosima brevicornis* (7.5 percent).



FIG. 5. *Cannula gracilis*, male. With the first generation, the population density of this bivoltine species is higher in the protected zones than in the burnt savanna, whereas the reverse is true of the second generation. (See also Fig. 21.)

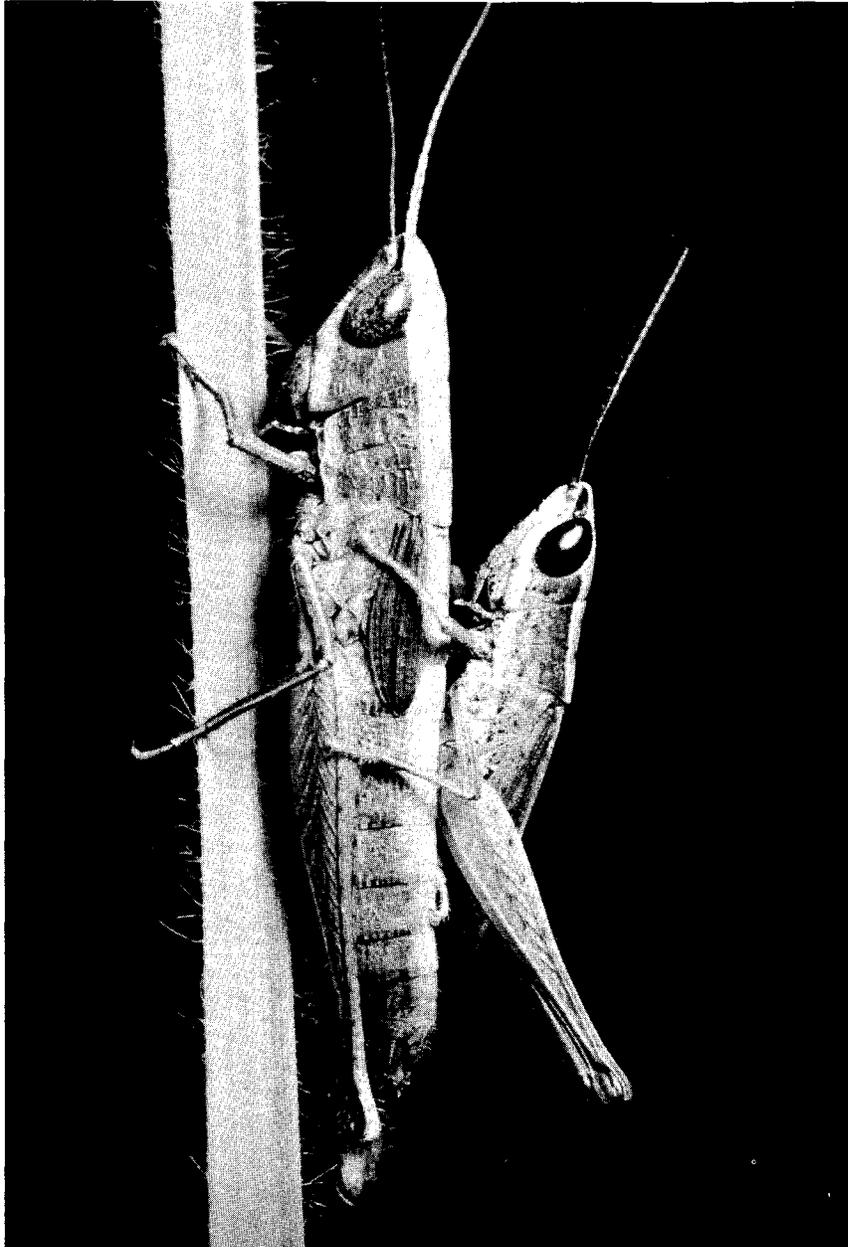


FIG. 6. *Rhabdoplea munda*, The large winged male is copulating with a small winged female. This species is eliminated by burning, but prospers in the unburned areas. (See also Fig. 22.)

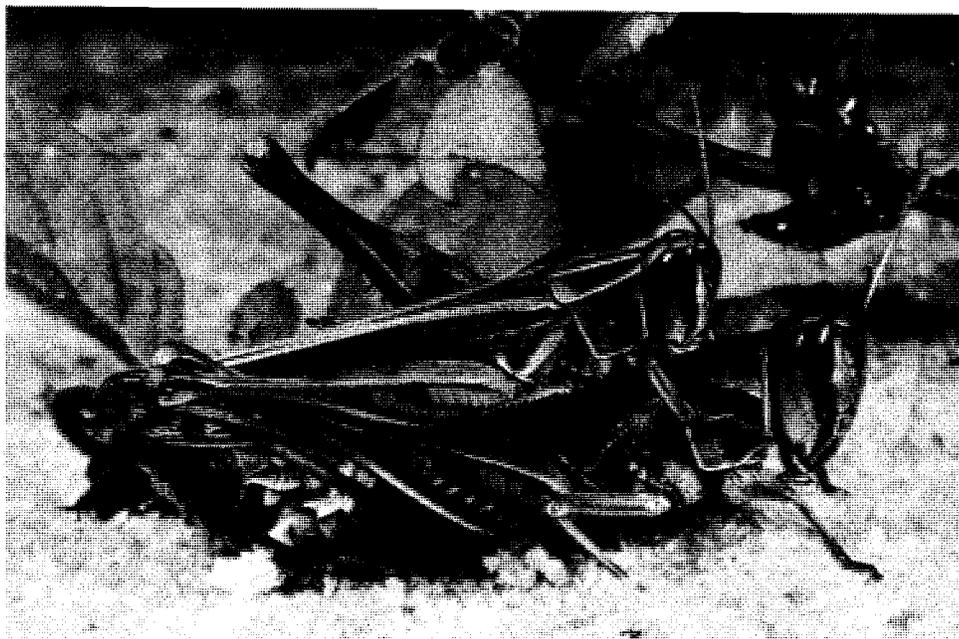


FIG. 7. *Tylotropidius didymus*, in copula. This species likes to sun itself, which perhaps explains its preference for the burned savanna. (See also Fig. 16.)

Out of a total of 38 species, the 11 forbivorous species represent 14.4 percent of the grasshoppers whereas the grass eaters are distributed as follows: 48 percent Acridinae (with eight species), 28.8 percent Gomphocerinae (with nine species), and 8.1 percent of other subfamilies (with 10 species).

Flight in front of the fire:—Because of their abundance, size and mobility, the acridids are the most conspicuous insects to flee the fire. They jump at random several tens of meters in front of the flames. Only when the acridids are near the fire do they move in its direction of progression.

This general behavior of the acridids in front of the fire depends on the intensity and area of the fire, factors dependent in their turn on the season, the rockiness of the terrain and its slope, the direction and speed of the wind, and on the thickness of the dry litter which is itself dependent on the date of the preceding fire.

When the fire starts, the insects flee rapidly, and one finds practically none in the cinders behind the curtain of flames, concentrating the fauna in front of it. As the population becomes dense and the distance from their origin becomes greater, more and more attempt to return. The more adept profit by the least occasion to pass

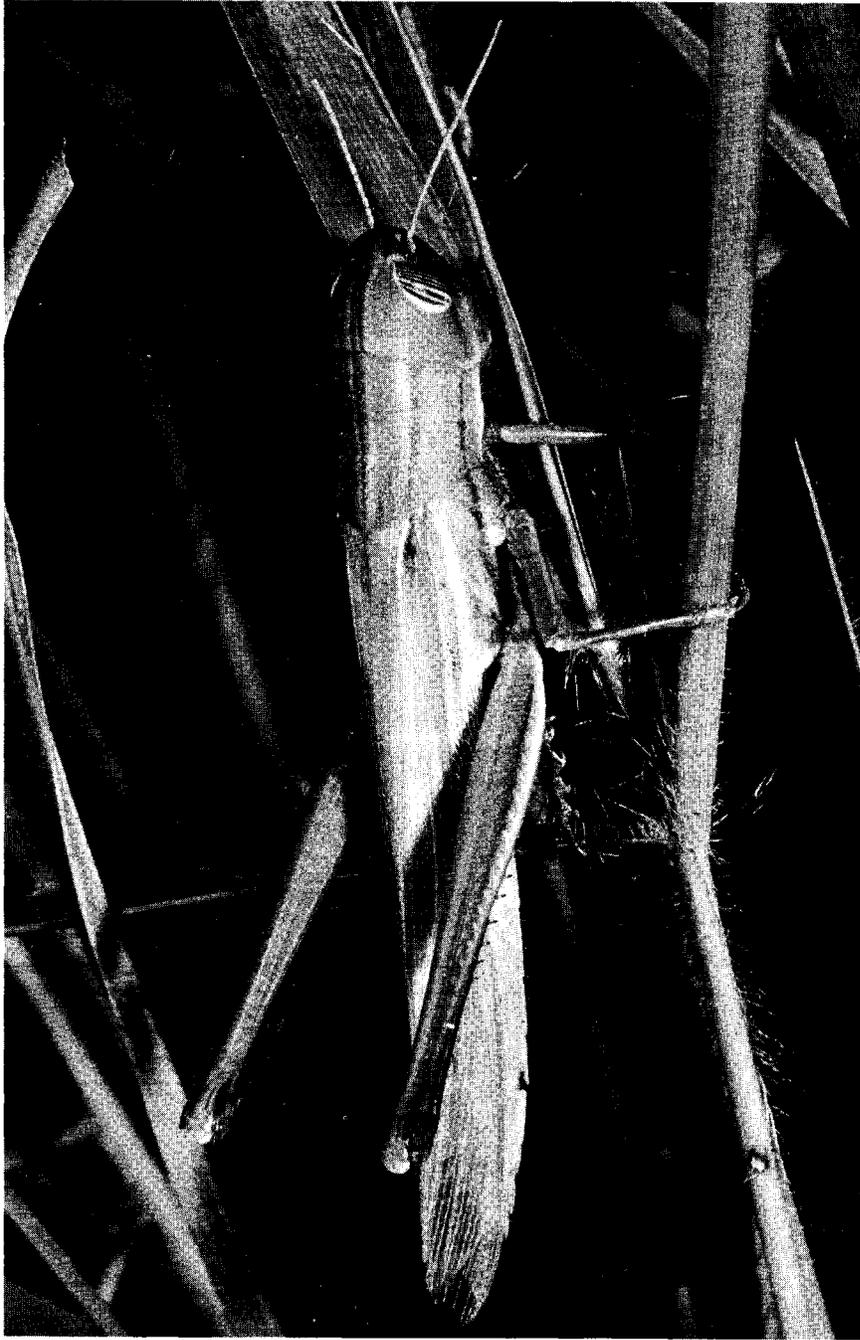


FIG. 8. *Chloroxyrrhopes virescens*, female. The nymphs of this species are more numerous in the burned savanna than in the protected zones although the females lay their eggs at the end of the rainy season, well in advance of the fire. (See also Fig. 13.)

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TABLE 3. LEVEL OF THE MAIN ACRIDID SPECIES PER 1000 M² AT DIFFERENT PERIODS

	A	B	C	D	E	F
<i>Tanita breviceps</i>	16.0	12.0	5.6	—	7.1	5.3
<i>Leptacris kraussi</i>	2.4	—	—	—	1.9	—
<i>Leptacris violacea</i>	1.6	—	—	1.1	2.8	—
<i>Tristria</i> spp.	52.0	5.3	3.4	73.3	63.0	579.8
<i>Petamella prosternalis</i>	8.0	—	—	3.3	12.1	7.3
<i>Eucoptacra anguliflava</i>	1.6	—	0.4	—	2.6	0.4
<i>Bocagella acutipennis</i>	2.4	—	—	—	0.7	7.3
<i>Acorypha</i> spp.	22.4	5.3	9.9	10.0	34.0	6.9
<i>Tylotropidius patagiatus</i>	7.2	—	—	—	9.5	8.5
<i>Tylotropidius didymus</i>	12.8	8.0	12.0	5.6	21.5	0.8
<i>Catantopsilus taeniolatus</i>	73.6	6.7	9.5	47.8	71.0	40.4
<i>Catantops</i> spp.	1.6	—	0.4	—	4.7	0.4
<i>Acridoderes strenuus</i>	1.6	—	1.7	5.6	3.3	3.6
<i>Parga cyanoptera</i>	1.6	8.0	4.7	7.8	1.9	3.6
<i>Machaeridia bilineata</i>	171.2	76.0	50.3	94.4	327.6	101.4
<i>Cannula gracilis</i>	48.8	1.3	3.4	22.2	30.3	8.5
<i>Rhabdoplea munda</i>	72.0	13.3	2.2	97.8	48.0	320.0
<i>Orthochtha brachycnemis</i>	97.6	72.0	371.1	225.6	137.5	107.1
<i>Orthochtha</i> spp.	8.8	4.0	52.5	3.3	21.8	2.8
<i>Coryphosima brevicornis</i>	72.8	22.7	37.0	36.7	57.8	36.4
<i>Gymnbothrus</i> spp.	—	2.7	8.2	—	—	—
<i>Heteropternis thoracica</i>	2.4	—	3.4	—	0.2	—
<i>Gastrimargus ochraceus</i>	2.4	—	—	—	1.7	0.4
<i>Gastrimargus</i> spp.	1.6	—	8.6	—	3.1	2.4
<i>Chromotruzalis liberta</i>	8.0	—	3.4	—	13.7	2.0
<i>Mesopsis abbreviatus</i>	20.8	—	14.2	10.0	11.6	6.1
<i>Mesopsis laticornis</i>	2.4	1.3	2.2	—	12.8	0.4
<i>Azarea lloydi</i>	14.4	5.3	7.7	1.1	41.4	0.4
<i>Brachycrotaphus buttneri</i>	41.6	—	9.5	7.8	34.8	3.2
<i>Anablepia granulata</i>	49.6	10.7	36.6	21.1	47.8	17.4
<i>Dnopherula bifoveolata</i>	37.6	28.0	24.5	5.6	101.1	8.5
<i>Dnopherula</i> sp.	—	2.7	—	—	9.7	1.2
<i>Dnopherula obscura</i>	110.4	9.3	109.7	34.4	196.4	184.2
<i>Faureia milanjica</i>	1.6	—	0.9	—	4.3	—
Total Acridids	970	300	794	717	1355	1492
Sampled Area (in m ²)	1250	750	2325	900	4225	2475

A = population of savanna burned one year earlier. B = population less than 48 hours after fire. C = population of burned savanna, one to five weeks after fire. D = population of unburned savanna near burned savanna, in January–February. E = population of the three last months of the year in burned savanna. F = population of last three months of the year in non-burned savanna.

through the curtain of flames: zones of *Loudetia simplex* with thin vegetation, rocky outcrops, or even a little gust of wind. The main chance of survival for poor flyers or non-flyers (young forms and brachypterous adults) is to return as quickly as possible, otherwise fatigued by flight, they will finally be caught by fire. Where a thin forest gallery interrupts the fire, the last conflagration is often spectacular because of the large grasses in the strip (notably *Andropogon macrophyllus*). At these occasions one can find savanna grass-

hoppers, even strictly grass eaters, on the soil of the forest where they would never go otherwise.

When the flames come to a recently burned zone, they die rapidly, and the young grass shoots are invaded by the insects which preceded the line of fire. This shows the importance of the parcelling of the burn on the spread and density of the fauna. One large fire is much more severe for insects than a number of limited fires over several days. Descamps and Wintrevert (1966) show, besides, that after Tetefort: ". . . setting generalized and simultaneous fires in the whole country was at one time the only real arm the Aborigines had against the migrating locusts in Madagascar." This peculiarity of small fires, their feeble power of destruction, is reinforced by the rapid invasion of burned zones starting with the nearest spared areas.

For strong flyers, particularly *Machaeridia bilineata*, choices of escape are numerous, and they often choose the moment when rocky ledges interrupt the line of fire to return. They are, by contrast, the principal victims of the kites who are probably attracted from afar by the smoke towards this concentration of agitated insects (Fig. 9).

Predation by raptorial birds:—Among the 23 insects, all Orthopterans in the larger sense, found in a stomach of *Butastur rufipennis* (killed by L. Bellier) from the fire of I-24-66, there were twelve grasshoppers of large size (at least 30 mm) (one female *Acorypha karschi*, one female *Tylotropidius didymus*, two females and one male *Tylotropidius patagiatus*, one female *Gastrimargus procerus*, two females *Orthochtha brachycnemis*, and four indeterminable ones).

Out of 13 stomachs of *Milvus migrans*, studied under the same circumstances, five contained respectively 21, 19, 13, four, and three acridids. The other prey were essentially crickets, long-horned grasshoppers and mantids (Gillon and Roy, 1968). The principal contents were debris of oil-palm seeds, fruits of *Elaeis guineensis*.

Out of a total of 235 insects, there were 60 adult acridids, three times as many females as males: one female *Tanita breviceps*, one female and one male *Tristria discoidalis*, one female *Eucoptacra anguliflava*, one female and one male *Acorypha karschi*, one female



FIG. 9. Concentration of kites in the smoke of a January fire.

and two male *Catantopsilus taeniolatus*, 20 females and eight males *Machaeridia bilineata*, one female *Cannula gracilis*, one male *Ocnocerus diabolicus*, one female and one male *Rhabdoplea munda*, one female *Gastrimargus africanus*, one female *Chromotruxalis liberta*, one female *Azarea lloydi*, five female and three male *Dnopherula bifoveolata*, and two female and one male *Dnopherula obscura*.

All these individuals, even the two *Rhabdoplea munda* are macrop-
terous, indicating that it is mainly the insects which flee the fire

by flying which are captured. The *Machaeridia bilineata* constituted almost one half of these acridids. *Butastur rufipennis* only preys on larger species. *Acorypha karschi* females are the only prey common to these two birds. These differences are not necessarily a question of size, for they could also be due to a difference in flight behavior in these acridids.

The stomach contents of a kite killed by J. M. Thiollay on the X-12-69 after an early fire, when the majority of univoltine acridids are not yet adults, is essentially constituted by partially burned nymphs (*Tristria* sp., *Macheridia bilineata*, *Dnopherula bifoveolata*). When few acridids are flying, the kites are more scavengers than predators.

Other falcon-like birds in the Lamto region also feed on acridids. These are essentially, from J. M. Thiollay, hunting birds, *Accipiter badius*, *Aviceda cuculoides*, *Falco ardosiaceus*, and above all *Kaupifalco monogrammicus* which captures large adult acridid species of such genera as *Tylotropidius*, *Ornithacris*, and *Acridoderes*, or, in the rainy season, species of *Chloroxyrrhopes* and *Homoxyrrhopes*. Fire favors this predation by displacing the insects.

The strygidiform raptorial birds also can feed on acridids, but tettigonids represent a greater portion of their diet. Aside from *Lissotis melanogaster* (Otidae) few other birds attack acridids. One sometimes finds them in the stomachs of certain meropids: *Coracias cyanogaster*, or more rarely, *Aerops albicollis*, and *Eurystomus ater*. These are always small acridids.

Acridids behind the fire:—Mortality. Following the intense fire of I-18-65, an average of five per 100 m² burned acridids and up to four per 25 m² were found (seven adults and nine nymphs in 300 m² sampled). The collections were situated in the first 100 meters of the burn, thus where the fauna is little concentrated, but the fire intensive and continuous. For these same 300 m², the number of live acridids captured was 27 (nine adults and 18 nymphs).

We don't pretend to give quantitative data on the fauna before fire, but, in the zone left unburned behind the origin of the fire of I-25-65 (which thus did not receive an influx of insects), 77 adults and 99 nymphs were collected on 150 m². Near the origin of the fire, about 85 percent of the immature and adults acridids flee, and

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of those that go through the flames, about two-thirds live. It is doubtful that burned insects were missed since all found were in rather good condition. The raw results, for 100 m² are as follows:

	acridids in unburned zones	acridids burned	acridids remaining alive	acridids fleeing
adults	51.3	2.3	3.0	46.0
nymphs	66.0	3.0	6.0	57.0
total	117.3	5.3	9.0	103.0
in percent				
adults		4.5%	5.8%	98.7%
nymphs		4.5%	9.1%	86.4%
total		4.5%	7.7%	87.8%

Correction of the percentage of nymphs burned would almost double this toll, because of the difficulty of finding the smallest ones and likewise, the percentage of adults remaining, for their flight is greater in denuded terrain. Raptorial birds capture only a small part of individuals considered here as "fleeing". As suggested by other authors, fire is not directly very destructive to acridids (Joyce, 1952; Robertson and Chapman, 1962).

Adults of 14 species of grasshoppers have been found after the different fires (*Catantopsilus taeniolatus*, *Machaeridia bilineata*, *Canmula gracilis*, *Rhabdoplea munda* (micropteran form), *Orthochtha brachycnemis*, *Orthochtha nigricornis*, *Coryphosima brevicornis*, *Gymnobotrus linea-alba*, *Heteropternis thoracica*, *Mesopsis abbreviatus*, *Mesopsis laticornis* (Fig. 10), *Brachycrotaphus buttneri*, *Dnopherula bifoveolata*, and *Dnopherula obscura*). In addition, nymphs of eight species were collected dead and charred (*Tristria* sp., *Acridoderes sirnuus*, *Parga cyanoptera*, *Canmula gracilis*, *Rhabdoplea munda*, *Orthochtha brachycnemis*, *Coryphosima brevicornis*, and *Anablepia granulata*).

This list is not complete, and it should be noted that the largest species are not represented (*Tylotropidius* spp., *Acorypha* spp., *Catantops* spp., *Ornithacris* spp., and *Chromotruxalis liberta*).

The experimental fire of April 7, 1965 was preceded the same day by six collections of 25 m², and followed by an identical series, the next day in the same place, both at 200 m from the fire break where the fire began. On 150 m² before the fire 177 acridids (16 adults, of which seven were *Rhabdoplea munda* micropterans and 161 nymphs, of which 73 were *Orthochtha brachycnemis* were found).

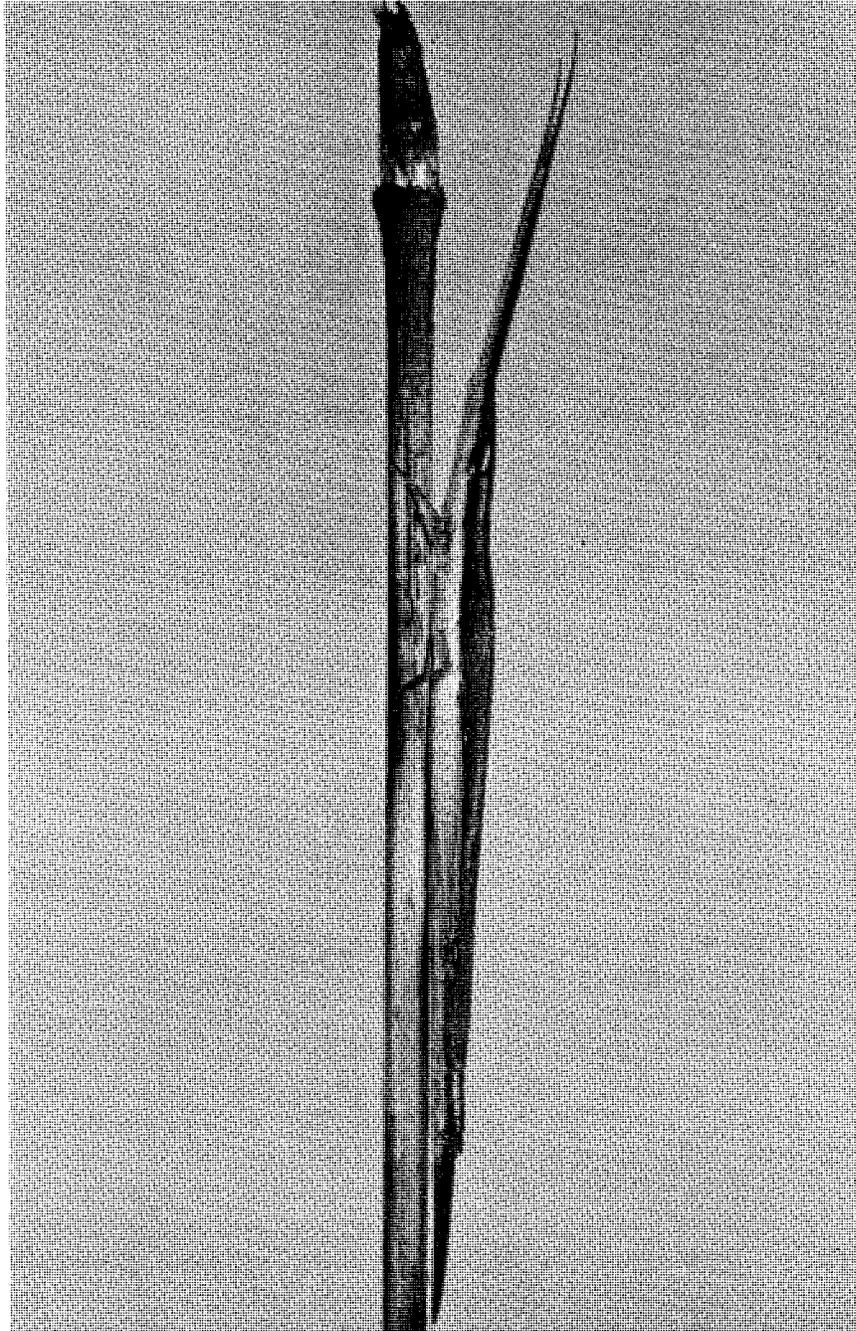


FIG. 10. *Mesopsis laticornis*, male. This species blends in with the half burned stubble that remains underneath in the burned savanna. They disappear from the areas protected from the fire. (See also Fig. 28.)

After the fire, 23 acridids (two adults and 21 juveniles) were found, or only 13 percent of the pre-fire population.

This suggests that there is a gradient of densities after fire, with a minimum at its origin and a maximum at its end.

Fire is set at a trail or a fire break, and collections are generally made near them since men and materials are brought in on them, explaining the illusory poverty of the collections the day after fire.

Density gradient. Two series of collections were made near the end of the burn.

The fire of January 13, 1964 went out that night, having gone a little more than 0.5 km. The fauna was sampled the next day at 50 to 100 m behind the end of the burn. Comparing the results to those of a single collection of 100 m² in the same zone one week earlier, one finds 85 acridids per 100 m² before fire (24 adults and 61 nymphs, of which 34 are *Rhabdoplea munda*) and 33 acridids per 100 m² the day after fire (14 adults and 19 nymphs). This is about 40 percent of the initial numbers or 58 percent of the adults and 31 percent of the nymphs.

The collections of 13 and 14 January 1966, before and after fire, were made in a *Loudetia simplex* zone, a grass which often burns poorly. Fire stopped there after having gone two km down the length of the trail. On 150 m² sampled there were 134 acridids before fire (91 adults and 43 juveniles, of which 25 were *Orthochtha brachycnemis*) and 116 after fire (110 adults and 6 nymphs). There was thus an increase in the adult density (121 percent were found), but a decrease in juveniles (14 percent were found).

The results of these different fires show a relationship between the distance traveled by the fire and the density of acridid adults the day after. The different effect on nymphs can be explained by their lesser ability to escape.

Species present. Collections the day after fire are generally too sparse to indicate the relative abundance of the species. We will thus group together the results of different fires to obtain an approximate spectrum of the acridids inhabiting the cinders and burned fields the day after fire. The collections used are the following: 300 m² on I-14-64, 300 m² on I-2-65 and I-19-65 and 150 m² on I-14-66 (Table 3, column B).

Only four species were found in all three series of collections (*Machaeridia bilineata*, *Orthochtha brachycnemis*, *Coryphosima brevicornis*, and *Dnopherula bifoveolata*), but 12 others were absent in only one of the three (*Tanita breviceps*, *Tristria marginicosta*, *Acorypha karschi*, *Catantopsilus taeniolatus*, *Parga cyanoptera*, *Rhabdoplea munda*, *Orthochtha nigricornis*, *Gymnbothrus linea-alba*, *Azarea lloydi*, *Anablepia granulata*, *Dnoperula* sp., and *Dnoperula obscura*).

Note that *Gymnbothrus linea-alba* appear in the newly burned zones, whereas they couldn't be found in the same areas before fire.

The five dominant species include as before fire: *Machaeridia bilineata* (25.3 percent), *Orthochtha brachycnemis* (24.0 percent), and *Coryphosima brevicornis* (7.6 percent); but also *Dnopherula bifoveolata* (9.3 percent) and *Rhabdoplea munda* (4.4 percent). In contrast, *Dnopherula obscura* and *Catantopsilus taeniolatus* become more secondary species.

Out of 24 species found after fire, the five non grass-eaters represent 11.1 percent of the total, whereas the grass-eaters are divided as follows: 67.1 Acridinae (with nine species), 19.1 percent Gomphocerinae (with six species), and 2.7 percent of diverse subfamilies (with four species). Compared to the situation before fire, the dominance of the Acridinae is again reinforced.

After the late fire of April 1965, only two acridid adult males were found on 150 m² searched, one *Machaeridia bilineata*, and one *Gymnbothrus subparallelus*. Before as after the fire, more than one half the nymphs are *Orthochtha brachycnemis*.

Thus, while the radical change of the habitat due to fire thus entails only unimportant specific changes in the acridid population as immediate effects, the largest change is in the density of the population.

MODIFICATION OF THE POPULATION AFTER FIRE

In the burned zones:—Weekly development. Collections made between one week and one month after the burning show an important development of the relative specific composition in this habitat. In 1964, series of weekly collections allow us to follow this transformation for the most abundant species. The weekly develop-

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ment of the adult densities per 100 m², between zero and five weeks after fire is as follows:

<i>Tylotropidius didymus</i>	0.0, 0.3, 1.0, 2.5, 2.7, 1.0
<i>Machaeridia bilineata</i>	0.3, 2.7, 12.0, 11.0, 4.0, 4.5
<i>Dnopherula bifoveolata</i>	0.3, 3.7, 0.5, 3.0, 2.7, 2.5
<i>Dnopherula obscura</i>	0.3, 5.7, 7.0, 29.0, 13.7, 14.5
Total of acridid adults	4.0, 18.0, 24.0, 60.5, 33.3, 32.0

All these species reached their maxima in less than five weeks. Due to eclosions, the results obtained for species having the largest proportion of nymphs are more irregular. These irregularities persist a long time because of the relative immobility of the nymphs:

<i>Orthochtha brachyemesis</i>	17.0, 7.0, 5.5, 52.5, 26.7, 19.0
<i>Coryphosima brevicornis</i>	3.7, 4.7, 4.0, 10.5, 6.7, 2.0

and for the total of acridids nymphs, the majority of whom are

<i>Orthochtha brachyemesis</i> :	23.3, 16.7, 17.5, 68.0, 30.7, and 23.0
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Among the less abundant species, *Tristria* spp. are found the day after fire, and one week later, but disappear later on. Adult *Parga cyanoptera* are constant at one per 200–300 m²; *Rhabdoplea munda* is rather numerous the day after fire, but is seldom found afterwards (one nymph in the fifth week). The nymphs of *Orthochtha nigricornis* appear from the third week. Adults of *Gymnobotrus linealba*, *Heteropternis thoracica*, *Gastrimargus africanus*, *Chromotruxalis liberta*, *Azarea lloydi*, and *Faureia milanjica* are found from time to time during this period. All *Mesopsis abbreviatus* found were nymphs, whereas all *M. laticornis* were adults.

Species present. Disregarding the collections of the day after fire, one obtains a glimpse of the relative abundance of acridid species which populate the freshly burned savanna by combining the results of the first five post-fire weeks of different years. This represents the maximum period before the March wave of eclosions whose relation to fire necessitates a special analysis.

The collections covered 2,325 m². The results, per 1,000 m² are presented in column C of Table 3. During the 5 years of the study, a dozen species were regularly found in the burned zones at the end of the dry season (*Tylotropidius didymus*, *Catantopsilus taeniolatus*, *Machaeridia bilineata*, *Orthochtha brachyemesis*, *Orthochtha nigricornis*, *Coryphosima brevicornis*, *Chromotruxalis liberta*, *Mesopsis abbreviatus*, *Brachycrotaphus buttneri*, *Anablepia*

granulata, *Dnopherula bifoveolata*, and *Dnopherula obscura*). Other species, only missing in one or two series, can still be considered as frequent at this time (*Tanita breviceps*, *Acorypha karschi*, *Cannula gracilis*, *Gymnobotrus linea-alba*, *Heteropternis thoracica*, *Gastrimargus africanus*, *Mesopsis laticornis*, and *Azarea lloydi*).

Certain very characteristic species of burned savanna don't appear in the collections with any regularity: (*Leptacris kraussi*, the majority of the Cantantopinae, (e.g. *Exopropacris modica*), *Orthochtha bisulcata*, *Gastrimargus ochraceus*, and *Fauereia milanjica*).

Nymphs of *Gastrimargus* spp. collected at this time in burned savanna are at the first stages of their development, and the majority of them belong to the species *G. africanus*.

The five dominant species represent 78.1 percent of the total number of acridids. These are, by order of decreasing importance: *Orthochtha brachycnemis* (46.7 percent), *Dnopherula obscura* (13.8 percent), *Orthochtha nigricornis* (6.6 percent), *Machaeridia bilineata* (6.3 percent), and *Coryphosima brevicornis* (4.7 percent). The level of *Anablepia granulata* is about the same as *Coryphosima brevicornis*. The nymphs of *Orthochtha bisulcata* and *O. nigricornis* are not distinguishable, but the former's adults are so rare that the lumping of the nymphs should not increase the numbers obtained for *O. nigricornis* very much.

As before the fire, *Dnopherula obscura* and *Coryphosima brevicornis* occupy the second and fifth positions respectively with a relative importance greater than before the fire. *Machaeridia bilineata* decrease in importance whereas *Orthochtha* sp., already important during fire, now constitute the dominant element of the acridid population, but are almost exclusively represented by nymphs. In spite of the great variety of species of acridids in this habitat, more than half the individuals belong to the genus *Orthochtha*.

Two pre-fire dominants no longer figure among the five most important species, *Catantopsilus taeniolatus* (1.2 percent) and *Rhabdoplea munda* (0.3 percent). The latter species almost disappears completely, and the only adults found are macropterous. The micropterous individuals were decimated after the fire. The progeny of these few adults will be practically nonexistent in the burned zones.

Species more abundant after than before fire are rare due to flight and fire-caused mortality, and also because the mortality of adults is generally not compensated by eclosions at this time (except in certain species such as *Orthochtha* spp.). Despite this, *Parga cyanoptera*, *Gymnobotrus linea-alba*, *Heteropternis thoracica*, and *Gastri-margus africanus* are somewhat more abundant. The slight decrease in *Tylotropidius didymus* and *Dnopherula obscura* shows that the increase of the population has almost compensated for the lowering of density by fire and mortality of adults.

The abundance of the different sub-families are about the same as before, even though the forbivorous acridids (nine species) only represent five percent of the total. The grass-eaters are 66.7 percent Acridinae (10 species), 25.9 percent Gomphocerinae (eight species), and 2.4 percent others, mainly Oedipodinae.

The weekly proportion of forbivorous may be linked to the decreased quantity of forbs in the burned zones (Roland and Heydacker, 1963), but just the same, the majority of the Catantopinae thrive in the burned zones.

In the unburned zones:—The occupation of burned zones by the adults of certain species dictates their departure from the spared zones. Others hide in these spared zones, as noted by Descamps (1953) with regard to *Nomadacris septemfasciata*. Population movements depend on the respective size of the parcels, that is, the distance which an animal would have to travel to find the habitat it prefers.

If tufts of herbs remain in the burns, these vertical forms will attract acridids from the surroundings. *Mesopsis laticornis* flies from stubble to stubble, always avoiding the unburned areas, and this is particularly characteristic of the species.

The fauna of unburned parcels within burned savanna was counted twice. In both cases the spared zones were located near a depression.

On February 6, 1962, a little more than one month after fire, only 45 acridids (17 adults and 28 nymphs) remained on 100 m² in an area in a hollow 30 by 15 m. The presence of four *Tristria* spp. and nine *Rhabdoplea munda* is characteristic of unburned savanna as is the absence of all *Dnopherula* sp. and *Machaeridia bilineata*. The last two are very abundant at the same time in surrounding burned savanna where 155 acridids were found (120 adults and 35 young). Of these,

27 were *Machaeridia bilineata*, five *Dnopherula bifoveolata*, and 72 *Dnopherula obscura*, but not one *Tristria* spp. or *Rhabdoplea munda*. The other species present in the unburned area were *Dictyophorus griseus*, *Acorypha karschi*, *Catantopsilus taeniolatus*, *Parga cyanoptera*, *Cannula gracilis*, *Orthochtha brachycnemis*, *Coryphosima brevicornis*, and *Mesopsis abbreviatus*.

On January 21, 1965, three days after fire, the fauna of another patch of unburned herbs of less than 100 m² was counted by a single collection of 25 m². Only seven acridids were found there: one nymph *Rhabdoplea munda*, two adults and one nymph of *Coryphosima brevicornis*, two male *Brachycrotaphus buttneri*, and one nymph of *Anablepia granulata*. Its location near the origin of the fire partly explains the impoverishment of this parcel. Once again, neither *Machaeridia bilineata* nor *Dnopherula* spp. were found there, although they were present in the surrounding burned areas the previous day.

The situation is very different in extended unburned zones near burned ones depending on whether they are located behind or in front of the direction of the fire. In the former case, the changes are due principally to the departure of certain insects for the nearby burned area. In the latter, the same phenomenon is less detectable, because it would have been preceded by the influx of acridids fleeing in front of the fire.

The modification of the acridid population in the unburned zones by the attractiveness of the burned ones was analyzed with the aid of unburned collections in January and February, less than 50 m from the starting point of the fire. We will use the results of collections of 200 m² in 1963, 500 m² in 1964, 150 m² in 1965 and 50 m² in 1966; in all 900 m². The total animals collected per 1,000 m² can be compared to those populations studied in the preceding paragraph (Table 3D).

These four series of collections are regularly composed of the ubiquitous species, and those characteristic of the zones protected from fire (*Tristria discoidalis*, *Tristria marginicosta*, *Machaeridia bilineata*, *Cannula gracilis*, *Rhabdoplea munda*, *Orthochtha brachycnemis*, *Coryphosima brevicornis*, and *Anablepia granulata*).

The five dominant species, are, in order of decreasing abundance:

Orthochtha brachycnemis (31.5 percent), *Rhabdoplea munda* (13.6 percent), *Machaeridia bilineata* (13.2 percent), *Catantopsilus taeniolatus* (6.7 percent), and one or both of the two species of *Tristria*, (together 10.2 percent) whose nymphs aren't distinguishable, but whose adults are about equally abundant.

Orthochtha brachycnemis and *Machaeridia bilineata* are among the five dominant species in both unburned and burned zones, showing a certain unity of the population in the savanna.

Certain species seem rather indifferent to the large differences at this time between the burned and unburned zones. The densities of the population of *Coryphosima brevicornis* and *Mesopsis abbreviatus* are similar in the two biotopes.

It is, above all, in demonstrating the attraction of the burned zones for adults of certain species that the comparison between burned and unburned zones is instructive.

The low density in unburned zones, of species otherwise common elsewhere (*Tylotropidius didymus*, *Orthochtha nigricornis*, *Azarea lloydi*, *Dnopherula bifoveolata* or *Dnopherula obscura*, and in lesser amount, *Anablepia granulata*) is not less remarkable than the total absence of *Gymnobothrus linea-alba*, *Chromotruxalis liberta*, *Mesopsis laticornis*, and of all the Oedipodinae, because the last are among the least abundant species of the Lamto savanna. All these species are thus displaced from the unburned zones towards the burned.

In limiting our analysis of the unburned zones to the first 50 m from the burned savanna, we accentuated the differences with respect to the total savanna, because exchanges are easier when the "border" is nearer. Proof of this comes from small unburned zones in the midst of the burned savanna. These represent the opposite extreme from the surrounding population. Inversely, unburned zones adjacent to large zones, burned up to the forest, present an augmentation of the elements of unburned savanna, above all *Tristria* spp.

INFLUENCE OF FIRE ON THE FOLLOWING GENERATION

For purposes of clarity we will leave aside the transition period, and begin the study of the following generation in April and May. Indeed, during March, in burned as well as unburned savanna, the

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eggs of certain species (such as *Machaeridia bilineata*) have not yet hatched, whereas the presence of adults of annual species interferes with the first eclosions. In April-May, the majority of the adults of the dry season have disappeared and the wave of young of the beginning of the rains attains its maximum.

Let us consider what remains of the influence of the fire by the end of the year, when these juveniles become adults. We will use the burned savanna data from October, November, and December, rather similar among themselves and to the unburned zones. The differences between the data of September and October are very pronounced for these two types of habitats.

SPECIFIC STRUCTURE OF THE WAVE OF NYMPHS

The areas sampled in burned savanna are 1,125 m² in April and 1,825 m² in May, and in unburned savanna 1,050 m² and 1,350 m² respectively.

At this time of the year, practically all the juvenile acridids hatched after the fire. The juveniles which survived the fire become adults, since annual species are then at the end of their development, and the development of multivoltine species is rapid.

The differences between juveniles of the burned savanna about 4 months earlier and that of the unburned zones thus reflect the indirect influence of the fires. The adults, by contrast, will not be taken into consideration, because these are for a large part veteran acridids of the dry season on which fire would have had a direct effect. In the species *Chloroxyrrhepes virescens*, the adults which come from nymphs hatched after the first rains will be used.

In limiting ourselves to the species forming at least 90 percent of the nymph population, we can list in order of abundance, species of burned and unburned savanna.

The proportion of individuals collected in the burned savanna with respect to the total capture, indicates the preference of a species for one or the other type of habitat. The results are the following, going from the species most linked to the burned savanna, to those which are most linked to the unburned: *Azarea lloydi* (100.0 percent), *Mesopsis laticornis* (99.3 percent), *Dnopherula bifoveolata* and *Dnopherula* spp. (99.0 percent), *Chromo-*

truxalis liberta (98.1 percent), *Orthochtha* sp (93.9 percent), *Mesopsis abbreviatus* (88.0 percent), *Catantopsilus taeniolatus* (74.7 percent), *Chloroxyrrhopes virescens* (57.0 percent), *Tylotropidius patagiatus* (45.1 percent), *Orthochtha brachycnemis* (43.0 percent), *Coryphosima brevicornis* (42.3 percent), *Brachycrotaphus buttneri* (40.9 percent), *Anablepia granulata* (40.0 percent), *Amphiprosopia adjuncta* (31.8 percent), *Gelastorbinus africanus* (18.1 percent), *Tristria* spp. (9.5 percent), and *Rhabdoplea munda* (3.3 percent). The population of juveniles is slightly higher in the burned (53.3 percent of the total) than the unburned zones.

A group of 10 species strongly linked to the burned savanna is apparent, while only three species are strongly linked to the unburned zones, where they are the dominant species. *Dnopherula obscura* is a dominant species, but not very characteristic of either habitat because it is found equally in both. *Orthochtha brachycnemis* is more abundant in the unburned savanna, although it ranks third in the burned.

Among the less common species in which the young seem tied to burned savanna, let us cite the *Gymnbothrus linea-alba* (23 captured in the burned zones and none in the zones protected from fire), *Heteropternis thoracica* (22 and two captured respectively), *Gastrimargus africanus*, *Gastrimargus procerus* and *Gastrimargus ochraceus* (respectively seven, 15, four, and zero, three, zero), and *Faureia milanjica* (13 in burned savanna only).

Inversely, 16 young of *Eyprepocnemis plorans* came only from unburned zones.

The comparison of these results with those (columns C and D, respectively of Table 3) of January and February for the parental generations of the burned and unburned zones shows that the contrast between the two faunas accentuates with time.

In the group of species whose juveniles are linked to the burned savanna one finds at this time: *Azarea lloydi* (87.5 percent in burned savanna), *Dnopherula bifoveolata* (81.4 percent), *Tylotropidius didymus* (68.2 percent), *Acorypha* spp. (35.9 percent) *Orthochtha* sp. (94.1 percent), and *Mesopsis abbreviatus* (58.7 percent). The numbers of *M. laticornis* and *Chromotruxalis liberta* adults captured was not enough to calculate a percentage. Thus, the species of the

generation contemporary with the fire were less clearly linked to the burned savanna, except for *Orthochtha* spp. (*O. nigricornis* and *O. bisulcata*) which are already represented by juveniles at this time. *Acorypha* spp. goes from a preference for unburned savanna to a clear predominance in burned savanna, but its population is constituted of two species, *A. johnstoni* and *A. karschi*. Unfortunately, we don't know to which species to attribute the young eclosed in February.

Tristria spp. show an avoidance of burned savanna more sharply than the following generation, at least near the burned savanna, since only 4.4 percent were found there.

Rhabdoplea munda only represents 2.2 percent of the burned savanna population the day after January–February fires, but still is greater than what is left in April–May.

Besides *Acorypha* spp., two other species (*Catantopsilus taeniolatus* and *Machaeridia bilineata*) had a slight preference for the burned zones in the beginning of the year. This was reversed by the next generation. Inversely, the juveniles of *Orthochtha brachycnemis*, *Coryphosima brevicornis*, *Brachycrotaphus buttneri*, and *Anablepia granulata* which showed a slight preference for burned savanna in January–February, now are better represented in the unburned savanna. Nevertheless, the species with a clear response to the burned and unburned areas after the fire, differ at least as much in the next generation.

REPARTITION OF THE SPECIES AT THE END OF THE YEAR

During the 3 last months of the different years of this study, 4,225 m² were collected in burned savanna, and 2,475 m² in unburned.

It is during this period that the nymphs of the preceding section become adults. With the exception of several annual species with rapid development (*Chloroxyrrhepes virescens* and *Gelastorhinus africanus*) which are no longer found by the end of the year, the majority of the acridids from the months of October to December are those hatched in April and May arriving at the end of their development. We would like to know if the repartition occurs by differential mortality or migration.

If the species most common as a function of their preference for burned savanna are classified in decreasing importance, we obtain from Table 3, columns E to F: *Azarea lloydi* (99. percent), *Mesopsis laticornis* (97. percent), *Tylotropidius didymus* (96.4 percent), *Catantops* spp. (92.3 percent), *Dnopherula bifoveolata* (92.2 percent), *Brachycrotaphus buttneri* (91.6 percent), *Dnopherula* sp. (89.0 percent), *Orthochtha* spp. (88.3 percent), *Chromotruxalis liberta* (87.3 percent), *Acorypha* spp. (84.6 percent), *Cannula gracilis* (78.1 percent), *Machaeridia bilineata* (76.4 percent), *Anablepia granulata* (73.3 percent), *Mesopsis abbreviatus* (65.5 percent), *Peta mella prosternalis* (63.4 percent), *Corphosima brevicornis* (61.4 percent), *Tanita breviceps* (57.3 percent), *Orthochtha brachycnemis* (56.2 percent), *Tylotropidius patagiatus* (52.8 percent), *Dnopherula obscura* (51.6 percent), *Catantopsilus taeniolatus* (38.5 percent), *Amphiprosopia adjuncta* (26.3 percent), *Rhabdoplea munda* (13.4 percent), and *Tristria* spp. (9.8 percent).

The groups occurring more than 80 percent in burned savanna are practically unchanged, as are those characteristic of the unburned savanna. Even though not belonging to these extreme groups, certain less characteristic species such as *Machaeridia bilineata* and *Tylotropidius patagiatus*, are also relatively consistent in their repartition.

In contrast, certain species have undergone a profound rearrangement since April–May. Thus, as in January–February, *Catantopsilus taeniolatus* is now found more abundantly in unburned savanna, while the graminivores are now leaving the unburned zones for the burned ones. The same type of redistribution can be observed in *Brachycrotaphus buttneri* and, to a lesser extent, in *Coryphosima brevicornis* and *Orthochtha brachycnemis*. Thus, these four species return to the January–February situation. All species showing this type of distribution have a macropteran adult phase during this period, which considerably augments their mobility. Of the species which do not have an annual cycle with adults only in the dry season, only *Rhabdoplea munda*, whose adults are micropterans, and *Orthochtha nigriconris* and *O. bisulcata* whose fidelity to burned savanna is very pronounced, do not undergo an important redistribution as a function of beginning of the year fire.

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TABLE 4. RELATIVE PROPORTIONS AND LEVELS PER 1000 m² OF THE NYMPHS OF THE MAIN ACRIDID SPECIES IN APRIL-MAY, IN BURNED SAVANNA AND UNBURNED ZONES
In burned savanna (5,225 acridid nymphs on 2,950 m²)

Species	Level per 1,000 m ²	%
<i>Dnopherula obscura</i>	378.2	21.4%
<i>Dnopherula bifoveolata</i>	283.3	16.0%
<i>Orthochtha brachynemis</i>	118.6	6.7%
<i>Azarea lloydi</i>	117.3	6.6%
<i>Catantopsilus taeniolatus</i>	74.9	4.2%
<i>Chloroxyrhepes virescens</i>	70.2	4.0%
<i>Acorypha</i> spp.	64.1	3.6%
<i>Machaeridia bilineata</i>	61.7	3.5%
<i>Tristria</i> spp.	59.3	3.3%
<i>Mesopsis laticornis</i>	58.0	3.3%
<i>Dnopherula</i> sp.	43.4	2.4%
<i>Tylotropidius patagiatus</i>	41.7	2.4%
<i>Coryphosima brevicornis</i>	41.3	2.3%
<i>Catantops</i> spp.	41.3	2.3%
<i>Tylotropidius didymus</i>	38.6	2.2%
<i>Orthochtha</i> spp.	27.5	1.6%
<i>Chromotruxalis liberta</i>	21.7	1.2%
<i>Amphiprosopia adjuncta</i>	19.3	1.1%
<i>Anablepia granulata</i>	13.6	0.8%
<i>Gelastorhinus africanus</i>	12.9	0.7%
<i>Mesopsis abbreviatus</i>	9.2	0.5%
<i>Brachycrotaphus buttneri</i>	9.2	0.5%
TOTAL	1605.3	90.6%
In unburned zones (3,723 Acridid nymphs on 2,400 m ²)		
<i>Tristria</i> spp.	567.9	36.6%
<i>Rhabdoplea munda</i>	269.2	17.4%
<i>Orthochtha brachynemis</i>	157.5	10.2%
<i>Dnopherula obscura</i>	156.7	10.1%
<i>Gelastorhinus africanus</i>	58.3	3.8%
<i>Coryphosima brevicornis</i>	56.3	3.6%
<i>Chloroxyrhepes virescens</i>	52.9	3.4%
<i>Tylotropidius patagiatus</i>	50.8	3.3%
<i>Amphiprosopia adjuncta</i>	41.3	2.7%
TOTAL	1410.9	91.1%

RELATIONSHIP OF THE REPRODUCTION CYCLES AND FIRE

DRY SEASON FIRES

The normal dry season fires pass at the beginning of the year, when the proportion of adults in the acridid population is at its maximum, but before the time of egg-laying. Despite what we have seen of the destructive effects of extensive fires on juveniles, these effects probably have not synchronized the species' cycles with the fires. They simply favor those species whose cycles are adapted to the rhythm

of fire, and thus influence the relative composition of the population. Indeed, differences persist all year in the burned and unburned habitats, even though the population density is similar at a given time. During the 3 months following fire (February, March, April), acridids are somewhat more abundant on the burned savanna while during the rest of the year, there are slightly more in the unburned zones (Fig. 11). Analysis by species as a function of the reproductive cycles will give a better picture of the real effects of fire.

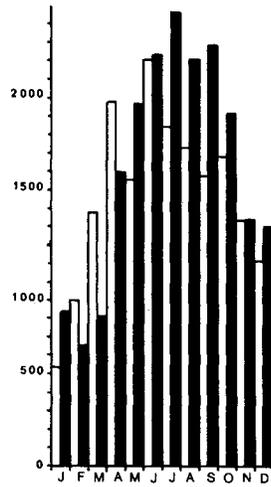
Interference with the Annual Cycles:—The effects of fire can be very different depending on whether species reproduce at the end of the dry season or the end of the rainy season.

Species which lay eggs at the end of the dry season usually undergo fire at the beginning of their adult life, and are thus able to escape by flying and recolonize the habitat. In addition, most females are immature at this time, and are not weighted down by eggs. Since fire passes before oviposition, the progeny of the species which prefer burned savanna are assured a certain type of habitat in which to develop. On the contrary, females which hide and lay eggs in the unburned zones always expose their progeny to the risk of having to develop in an unfavorable habitat, should late fire occur.

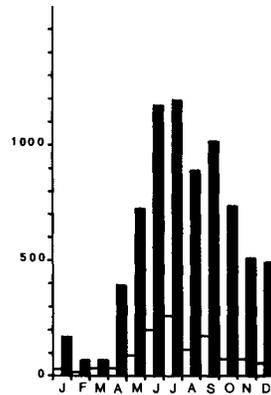
Tylotropidius didymus (Fig. 16), *Catantops spissus*, *Catantops stylifer* (Fig. 18), *Machaeridia bilineata* (Fig. 19), *Chromotraxalis liberta* (Fig. 26), *Mesopsis laticornis* (Fig. 28), *Azarea lloydi* (Fig. 29), *Dnopherula bifoveolata* (Fig. 32), *Dnopherula obscura* (Fig. 33), and *Fauereia milanjica* (Fig. 34) have a marked preference for burned savanna, and a reproductive cycle which synchronizes the appearance of immature adults with the greatest probability of fire. Both phenomena are induced by the dryness of the season. Among the ten species cited, only one, *Dnopherula obscura*, does not maintain a higher population in the burned zones (Fig. 33).

The structure of the populations of juveniles of this species was studied by measuring the size of the posterior femur on 824 individuals captured in May of different years (Fig. 35). Dividing these juveniles into three classes the average class has a femur size of five–six mm, and comprises about 70 percent of the total young of the species in both habitats. Even though they are always more

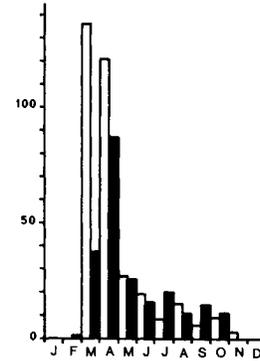
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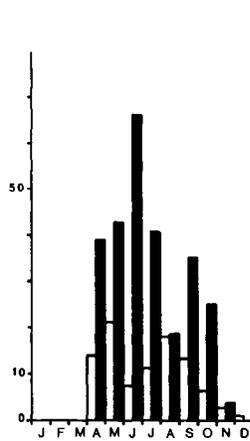
11. All acridids



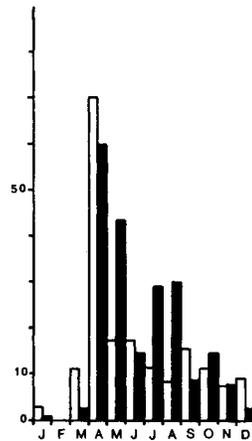
12. *Tristria* spp.



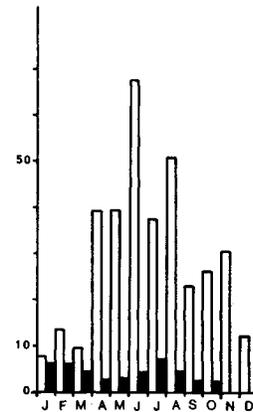
13. *Chloroxyrrhpes virescens*



14. *Amphiprosopia adjuncta*



15. *Tylotropidius patagiatus*



16. *Tylotropidius didymus*

Figs. 11-16. Comparative levels of the principal acridid species on burned savanna (open bars) and unburned zones (solid bars) where no burning has taken place for more than one year, per 1,000 m².

abundant in burned savanna, the largest, oldest individuals represent a smaller proportion in the burned zones than the unburned. They are also more evenly spread out than the youngest class, of which

more than 80 percent live in the burned savanna. These are the results of colonization by the parental adults of the burned savanna in preference to the unburned. The observed difference of the average age cannot be explained by differential growth, for this would tend to increase the speed of development in burned habitats because of thermal or trophic conditions. Finally, important mortality of the juveniles in the unburned zones is contradicted by the abundance of the species at the end of the year (Fig. 33).

Similar results are obtained for the same month with femur sizes of juvenile *Machaeridia bilineata*, and abundant species in both the burned and unburned savanna, but in this case the largest juveniles are more abundant in the unburned zones than the burned. The inverse is true of the younger classes, which, in comparison with *Dnopherula obscura*, accentuate the juvenile characteristic of the burned savanna population (Fig. 36). At the beginning of the period of laying, many *M. bilineata* could be found in the unburned zones. At least part of them have emigrated and laid their eggs in the burned savanna.

Tristria marginicosta appears to be the only species with a preference for unburned zones and with a similar cycle, the dry season fires coinciding with the adults. *Tristria discoidalis* does have a cycle of the same type, but more spread out in time, such that when fire occurs, one finds newly emerged young together with last instar nymphs of the preceding generation.

The adults of annual species which lay earlier than the preceding ones, well before fire, do not place the eggs with respect to burning, since, as noted, the probability of fire in unburned areas increases. If placement of eggs alone governed the future distribution of the juveniles one should not find large differences between the burned and unburned zones. However, our data show that although these species never attain the quasi-exclusive character observable of the preceding type, they are not indifferent to fires, even though their eggs are deeply buried and experience only negligible elevation of temperature during the fire.

Certain of these species, such as *Amphiprosopia adjuncta* (Fig. 14) and *Gelastorhinus africanus* (Fig. 20), are more abundant in the unburned zones. More *Chloroxyrrhypes virescens* close in the burned

savanna, but with the rapid appearance of mobile adults, the density is soon equal in the two habitats (Fig. 13); *Tylotrypidius patagiatus* has a similar cycle, but other factors must influence this evenly spread out micropteran, masking the effects of fire (Fig. 15).

In the annual species with well-marked cycles, the time of fires does not coincide with the period of maximum oviposition (except perhaps in *Tristria discoidalis* which hides in the unburned zones) or eclosion, but rather with the egg incubation period of rapidly developing species, or with the female sexual maturation period of others. The males generally appear shortly before the females, and have a maturation period of only a few days.

The annual cycle of *Gastrimargus africanus* is intermediate between the two preceding types, since development is rapid after the March–April eclosions, but the adults, which thus appear during the rainy season, do not attain maturity until the dry season. All the young individuals come from areas burned less than six months previously. Thus, egg-laying follows the fire, and may be induced by the appearance of denuded terrain. In support of this hypothesis, a few adults of the majority of Oedipodinae and of the closely related genus, *Gymnbothrus*, can always be found in recently burned zones. These “opportunistic” species can also be multivoltine, offering a more flexible cycle.

In order to illustrate more precisely the adaptive importance of the phenological harmony between development and the period of fires, it is necessary to study multivoltine species, and the effects of a late fire.

Interaction with Multivoltine Species:—Of the nine most abundant multivoltine species of the savanna, none disappear totally at any time, and only two in our collection (*O. nigricornis* and *M. abbreviatus*) are not represented the whole year as juveniles and adults. Consequently, fires cannot coincide exclusively with the egg period as is the case in certain annual species (Table 5).

The relative abundance in January of developmental stages for the nine most common multivoltine species (Table 5) shows that fire occurs most often at the same phenological moments as with the annual species: time of immature adults (*Catantopsilus taeniolatus*, *Cannula gracilis*, *Rhabdoplea munda*, and *Coryphosima brevicornis*),

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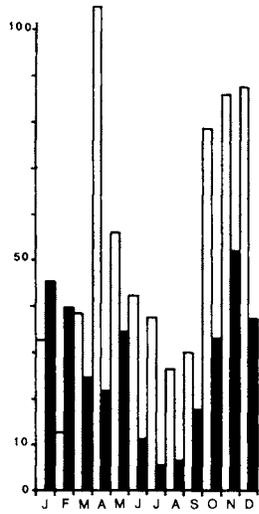
TABLE 5. IMPORTANCE OF DIFFERENT PHASES OF THE CYCLE OF MULTIVOLTINE SPECIES IN THE MONTH OF JANUARY, THE TIME OF FIRE. (++) = DOMINANT, + = AVERAGE, AND - = RARE)
Multivoltine species

	Eclosions	Nymphs	Immat. Adults	Mature Adults	Eggs
<i>Catantopsilus taeniolatus</i>	-	+	++	+	-
<i>Cannula gracilis</i>	-	+	++	+	-
<i>Rhabdoplea munda</i>	-	+	++	+	+
<i>Orthochtha brachynemis</i>	+	-	-	+	++
<i>Orthochtha nigricornis</i>	+	-	-	+	++
<i>Coryphosima brevicornis</i>	-	+	++	+	-
<i>Mesopsis abbreviatus</i>	+	++	-	-	-
<i>Brachycrotaphus buttneri</i>	+	+	++	++	+
<i>Anablepis granulata</i>	++	+	-	+	++

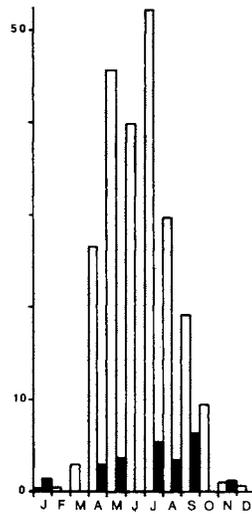
or the period of maximum eggs (*Orthochtha brachynemis* and *Orthochtha nigricornis*). However, these stages do not exclude others, and certain species do not follow this sequence. For example, *Brachycrotaphus buttneri* is represented at this time by mature adults, and the eggs of *Anablepis granulata* eclose at this time. The most contradictory cycle is that of *Mesopsis abbreviatus* which is mostly represented by juveniles of average size.

Detailed demography of multivoltine species with the aid of posterior femur size classes can elucidate their reactions to fire. Thus, *Anablepis granulata* in the burned savanna shows a large increase in the smallest juvenile class (femur size: 3-6 mm, the first three instars) in February (Fig. 37). If incubation takes 2 months, as in lab-rearing this increase would be due to the differential mortality of eggs or newly hatched, and not to ovipositions, since fire occurred less than 2 months earlier, before egg-laying. Besides, the adults are more evenly spread out. These results confirm the innocuousness of fire to acridid egg pods, even for relatively small species. The same measurement on the May population gives a different glimpse of the repartition (Fig. 37). Even though the most numerous juveniles (the 5-6 mm size class) must derive mostly from February eggs, and the adults from the juveniles of the same period, in May the unburned savanna has the greatest density of the youngest individuals. Thus the burned savanna would be favorable to the development of the juveniles, but does not particularly attract the adults of this stenophage species. The mobile adults are perhaps

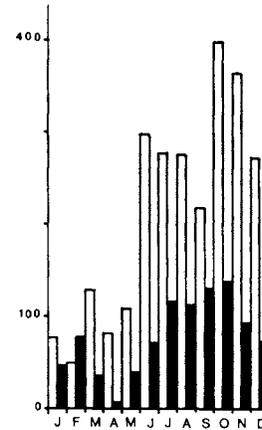
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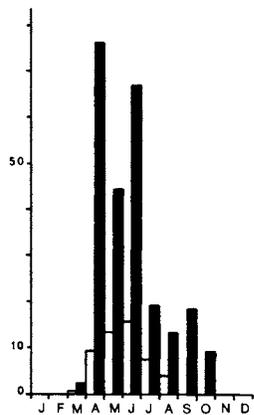
17. *Catantopsilus taeniolatus*



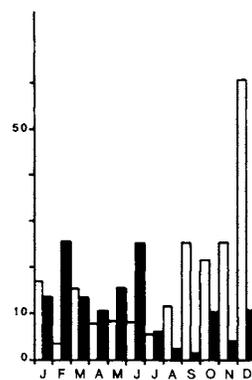
18. *Catantops* spp.



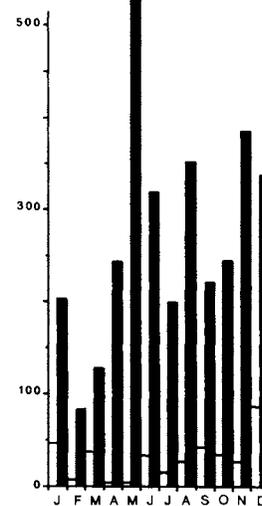
19. *Machaeridia bilineata*



20. *Gelastorhinus africanus*



21. *Cannula gracilis*



22. *Rhabdoplea munda*

Figs. 17-22. Same as Figs. 11-16, additional species.

less dependent than the young on the density of *Brachiaria* sp., their food.

For *Orthochtha brachycnemis*, with a much clearer biovoltage cycle than the preceding species, the January fires also occur during

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the egg phase. Here again, the demography of the young shows a disequilibrium, even more in favor of the smaller juveniles in the burned savanna (Fig. 37).

In May, in the unburned savanna, *Orthochtha* spp. are larger juveniles and adults of the February young. On the contrary, certain newly emerged nymphs already appear in the burned savanna, where the species occurs in greater density than in the unburned zones at the end of the year, as we have already seen.

CONSEQUENCES OF A LATE FIRE

The total number of acridids in the savanna burned late (IV-7-65) was compared to unburned savanna, and to January burns of the same year (1-18-65). The same area was collected (150 m² each month) for the same period (April to December). 1,291 acridids (174 adults and 1117 juveniles) were collected from the 1,350 m² after the late fire, and 2862 (367 adults, and 2495 juveniles) from the same area of savanna burned as usual in January. In both these cases, the proportion of adults is 13 percent. It is 11 percent under the same conditions in unburned savanna (272 adults and 2,147 juveniles) (Table 6).

TABLE 6. EXAMPLES OF ACRIDIDS COLLECTED BETWEEN APRIL AND DECEMBER IN 1965 IN UNBURNED SAVANNA (SNB), BURNED I/18/65 (SB), AND IN THE LATE BURNED ZONE ON IV/7/65 (SBT) OVER 150 M² PER MONTH

	<i>Univoltine species</i>		
	SB	SBT	SNB
<i>Tristria</i> spp.	101	76	1080
<i>Machaeridia bilineata</i>	738	374	260
<i>Chromotroxalis liberta</i>	28	0	0
<i>Mesopsis laticornis</i>	33	1	0
<i>Azarea lloydi</i>	62	8	0
<i>Dnopherula bifoveolata</i>	369	12	1
<i>Dnopherula obscura</i>	264	38	171
	<i>Multivoltine species</i>		
<i>Catantopsilus taeniolatus</i>	54	92	29
<i>Cannula gracilis</i>	23	27	15
<i>Rhabdoplea munda</i>	12	8	248
<i>Orthochtha brachynemis</i>	545	126	343
<i>Orthochtha nigricornis</i>	46	16	4
<i>Coryphosima brevicornis</i>	160	154	112
<i>Mesopsis abbreviatus</i>	16	29	16
<i>Brachycrotaphus buttneri</i>	30	6	5
<i>Anablepia granulata</i>	37	37	33
Total acridids	2862	1291	2419

The savanna burned late is thus generally less densely populated than the savanna burned in January: 45 percent of the savanna burned in the normal way. The ratios to normally burned savanna populations for each month from April to December are 4 percent, 43 percent, 65 percent, 69 percent, 44 percent, 52 percent, 33 percent, and 80 percent. The zone burned in April is thus emptied of its acridids, at least near the start of the fire where collections had been made, then repopulated to more than half the normal level, with a decrease at the end of development, but a clear regain in December, when the new adults appear.

In these collections, the five most important species are, in decreasing order of importance:

In savanna burned in January: *Machaeridia bilineata* (17 percent), *Orthochtha brachycnemis* (12 percent), *Dnopherula bifoveolata* (eight percent), *Dnopherula obscura* (six percent), and *Coryphosima brevicornis* (four percent).

In savanna burned late: *Machaeridia bilineata* (29 percent), *Coryphosima brevicornis* (12 percent), *Orthochtha brachycnemis* (10 percent), *Catantopsilus taeniolatus* (7 percent), and *Tristria* spp. (6 percent).

The dominance of the most abundant species is thus reinforced by late fire, and qualitatively, the spectrum of these species differs according to the date of fire. This might be explained by what we now know about the relationship between fire and the phase of the acridids' cycles.

The late burned zone first shows an increase in the species characteristic of unburned savanna, and an elimination of the adults of the annual species characteristic of burned zones (*Chromotraxalis liberta*, *Mesopsis laticornis*, *Azarea lloydi*, or *Dnopherula bifoveolata*). That fire makes the habitat more favorable to these species cannot compensate for the absence of egg-laying in these areas at the beginning of the year. The annual species are thus poorly represented in late burns, for it is too late for the burned savanna species to reproduce there, and the unburned savanna species which have already laid there, cannot subsist there.

Among the univoltine species least disfavored by late fire are *Tristria* spp. adults which prefer egg-laying in the unburned zones,

which this parcel was at the time of the January fires. In this zone, they already constituted 6 percent of the total during the first months of the year 1965.

The particularly late eclosions of the eggs of *Machaeridia bilineata* combine with the relative indifference of this species to burned or unburned habitats to explain the reinforcement of the numbers of this species in the late-burned area.

Fire decimates the juveniles of the typical annual species such as *Dnopherula obscura* which ecloses in the unburned zones at the beginning of April. This confirms the importance of not being juvenile at the time of fire.

One of the species more favored by the late fire is *Mesopsis abbreviatus* whose cycle has, as we have seen, the strange characteristic of producing a wave of juveniles just before the dry season fires.

At the beginning of April the populations of *Orthochtha* spp. are very vulnerable because they are almost entirely constituted of late-instar juveniles. In contrast, their well marked cycle makes the greatest-period of egg abundance coincide with the January fire. In the protected zone, near the experimental late fire, *Orthochtha brachycnemis* was the most abundant species. It represented 38.6 percent in the collections at the beginning of the year (362 individuals out of 939 in 600 m² collected), but less than 10 percent after the late fire. *Rhabdoplea munda*, like *Tristria* spp., lays in the yet unburned zone. They represent more than 15 percent of the total, but recently burned areas are unfavorable to the development of the juveniles of this species so that they disappear.

Out of season fires usually occur at a less favorable time in the reproduction of the acridids since the population is mostly juveniles, many of which die in the fire. In addition, the redistribution of the species by habitat preference is hampered by a lack of mobile adults. However, certain juveniles must move sufficiently to colonize the recently burned habitat, suggesting an abundance in the late burned habitat as compared to the unburned savanna, of species such as *Orthochtha nigricornis* (16 young), *Azarea lloydi* (eight young), or *Dnopherula bifoveolata* (12 young). This is also the best interpretation of the variations of the repartition of juvenile *Orthochtha brachycnemis* between February and May (Fig. 38).

The least affected species would thus be either those which did not flee the unburned habitat at the beginning of the year, or those which recolonize it after the fire.

If the coincidence of the fires with certain developmental stages is as important as our results suggest, several hypotheses can be advanced on the effects of August fires, during the little dry season. They should decimate *Machaeridia bilineata* as well as other annual species, whereas they would be less destructive to the adults of large species, such as *Chlorxyrrhepes virescens* or *Acorypha johnstoni*. The *Orthochtha* spp., then late in the development of the second generation would be, as in April, rather sensitive to these fires, whereas *Anablepia granulata* and *Coryphosima brevicornis*, which reproduce all year round, should present an unchanged sensitivity. *Catantopsilus taeniolatus* would be in the middle of the laying period, and should be moderately affected.

PROLONGED ABSENCE OF FIRE

A pocket depression in front of which fire stopped of its own accord in December 1961, has since been protected from fire. The collections of May 19, 1969 give a glimpse of the development of the acridid population under these circumstances (Table 7).

After this extended protection, the differences between the collections of 1963 and those of 1969 are less marked than those between the burned and unburned savanna from year to year. Thus, dominant species remain the same: *Rhabdoplea munda* and *Tristria* spp. (*T. discoidalis* and *T. marginicosta* always coexist). Their abundance is unchanged, but their dominance increases; they represent 68 percent and 72 percent of the total in the collections of 1969, but 59 percent and 62 percent of those of 1963.

Among the species which prefer burned savanna, two were found in 1963: *Tylotropidius didymus* and *Dnopherula obscura*. The first remains in 1969, still at a low density, but the second does not. *Machaeridia bilineata*, one of the most abundant species of the Lamto savanna, seems to have disappeared even earlier. This depression had not burned for several years prior to 1969.

Among other acridids which disappear are *Amphiprosopia ad-*

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TABLE 7. ACRIDIDS COLLECTED IN THE SAME DEPRESSION, CONTINUALLY PROTECTED FROM FIRE, IN JUNE-JULY 1963, AT LEAST TWO YEARS SINCE THE LAST FIRE, THEN IN MAY 1969. ALL COLLECTIONS WERE MADE ON AN AREA OF 100 M²

	VI-63	VII-63	VII-63	V-69	V-69
<i>Dictyophorus griseus</i>	2	—	—	—	—
<i>Pyrgomorphidae</i> , unknown sp.	—	—	—	1	—
<i>Spathosternum pygmaeum</i>	—	—	—	8	18
<i>Tristria</i> spp.	41	23	102	42	21
<i>Chloroxyrrhepes virescens</i>	4	—	—	—	—
<i>Epistaurus succineus</i>	—	—	—	16	—
<i>Eyrepocnemis plorans</i>	3	1	—	17	8
<i>Amphiprosopia adjuncta</i>	16	18	9	—	—
<i>Tyotropidius patagiatus</i>	6	3	5	3	6
<i>Tyotropidius didymus</i>	—	2	—	1	3
<i>Carydana agomena</i>	1	—	—	—	—
<i>Catantopsilus taeniolatus</i>	4	—	—	2	—
<i>Gelastorhinus africanus</i>	4	1	—	1	—
<i>Rhadoplea munda</i>	36	43	12	88	63
<i>Orthochtha brachynemis</i>	8	2	45	—	2
<i>Coryphosima brevicornis</i>	—	1	3	—	—
<i>Coryphosima stenoptera</i>	—	—	—	1	—
<i>Mesopsis abbreviatus</i>	—	—	3	—	2
<i>Amesotropis valga</i>	9	3	1	—	—
<i>Dnopherula obscura</i>	20	15	10	—	—
TOTAL	204	112	190	180	123

juncta, *Amestropis valga*, and to a lesser degree *Gelastorhinus africanus*, whose preference for unburned savanna is clearer (Fig. 14 and 20). For these species, several years is apparently an optimum time of protection.

Finally two species, *Spathosternum pygmaeum* and *Epistaurus succineus*, only appear after long protection. They live in the most humid parts even of burned savanna, and are always more frequent in the low Ivory Coast. This is also true for *Eyrepocnemis plorans* whose density increases from one collection to the other.

DISCUSSION

We have presented evidence that various species of this relatively homogeneous group of reputedly heliophilous acridids, show diametrically opposed reactions toward fire. Thus, despite the variations of behavior of several multivoltine species as a function of time since fire, the perpetuity these effects of fire has on the composition of the population allows the arrangement of the species according to their preference for burned or unburned savanna. This preference is expressed as the percentage of juvenile and adult individuals per unit

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area of burned savanna with respect to the sum of the totals of burned and unburned zones.

LESS THAN 10 PERCENT IN BURNED ZONES

Eyprepocnemis plorans

FROM 10 TO 20 PERCENT IN BURNED SAVANNA:

Rhabdoplea munda
Tristria discoidalis and *T. marginicosta*
Gelastorhinus africanus
Dictyophorus griseus

FROM 20 TO 30 PERCENT IN BURNED SAVANNA:

Amphiprosopia adjuncta

FROM 30 TO 40 PERCENT IN BURNED SAVANNA:

Amesotropis valga
Bocagella acutipennis hirsuta
Acridoderes strenus
Parga cyanoptera

FROM 40 TO 50 PERCENT IN BURNED SAVANNA:

Amphicremna scalata
Tylotropidius patagiatus

FROM 50 TO 60 PERCENT IN BURNED SAVANNA:

Leptacris violacea
Orthochtha brachycnemis
Coryphosima brevicornis
Petamella prosternalis
Anablepia granulata
Cannula gracilis

FROM 60 TO 70 PERCENT IN BURNED SAVANNA:

Dnopheruka obscura
Chloroxyrrhypes virescens

Catantopsilus taeniolatus

Mesopsis abbreviatus

FROM 70 TO 80 PERCENT IN BURNED SAVANNA:

Tanita breviceps
Eucoptacra anguliflora
Machaeridia bilineata
Brachycrotaphus butneri
Gastrimargus procerus

FROM 80 TO 90 PERCENT IN BURNED SAVANNA:

Dnopherula sp.
Carydana agomena
Orthochtha bisulcata and *O. nigricornis*
Acorypha karschi
Tylotropidius didymus
Chromotruxalis liberta

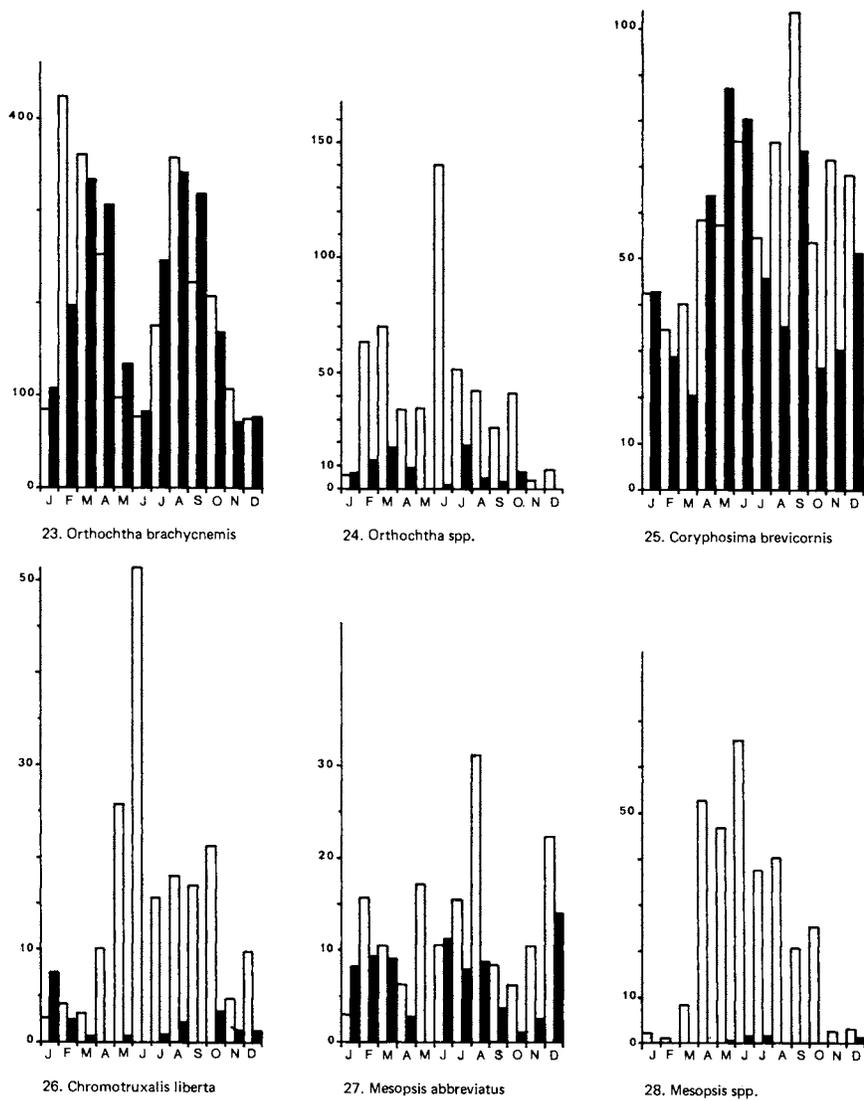
MORE THAN 90 PERCENT IN BURNED SAVANNA:

Spathosternum pygmaeum
Leptacris krasussi
Acorypha johnstoni
Catantops spp.
Gastrimargus ochraceus
Dnopherula bifoveolata
Exopropacris modica
Heteropternis thoracica
Gymmobothrus linea-alba
Mesopsis laticornis
Azarea lloydi
Faureia milanjica
Gastrimargus africanus

Thus, only one species, *Eyprepocnemis plorans*, which is common in secondary habitats, is found more than 90 percent in the unburned zones, whereas about 14 are represented by at least 90 percent in savanna burned less than one year previously; this reflects the heliophilous nature of the group.

This tendency is particularly marked in the Gomphocerinae of which only *Amesotropis valga* has a certain predilection for the unburned zones, even though it disappears when fire is absent for

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Figs. 23-28. Same as Figs. 11-16, additional species.

several years. The Oedipodinae and most geophilic acridids are also limited to the areas denuded by fire.

The micropteran acridids are favored by unburned habitats: *Tylotrypidius patagiatus*, a powerful jumper; *Amphiposopia ad-*

juncta, of which only the males can fly; *Dictyophorus griseus*, a geophilous species, and *Rhabdoplea munda*, which has seasonal micropteran forms.

Finally, the species with the most elongated forms (*Leptacris kraussi* and *L. violacea*, *Cannula gracilis*, *Chromotruxalis liberta*, *Mesopsis abbreviatus*, and *Mesopsis laticornis*) prefer the more open burned habitats even though they are generally phytophilous.

The dominant species of the unburned zones, *Rhabdoplea munda* and *Tristria* spp., have a uniform color of dried herbs. Nevertheless, this coloration is also found in *Cannula gracilis*, *Machaeridia bilineata*, and even *Azarea lloydi*, all very true to burned savanna.

Even though fire always destroys part of the insects directly, or by favoring predation, it is generally favorable to the great majority of acridids by periodically rejuvenating the habitat. It is after fire that the diversity of species is greatest. This indirect action of fire is, within certain time limits, a limiting factor for several species, but since in its absence the savanna would become forest, all the species of the grassy layer in this region of Africa owe their existence, to fire.

Our results as well as those of Joyce (1952) and Descamps and Wintrebert (1966) show that the eggs are not affected by fire, but we have not been able to support the latter's hypothesis of synchronization of the eclosions by fire. The populations of several of our species do not show a greater age spread in the unburned zones than in the burned ones.

If the mortality of juveniles is related inversely to the habitat temperature (Dempster, 1963), the great isolation of the burned habitat should be particularly favorable to nymphs. However, certain species, such as *Rhabdoplea munda* seem, probably for other reasons, to be unable to maintain a population of juveniles in the burned zones.

Immediately after fire, the temperature might play an important role because of the blackening of the habitat and all the acridids. It would be surprising if their internal temperature were not increased with the concomitant effects on their metabolism. Several young teneral green grass-colored nymphs of *Anablepia granulata* sit on the calcified substrate when not on young shoots of grasses.

A major conclusion is the great role of the habitat structure and physical factors in determining the specific composition of the herbal floor, that is, the alimentary resources.

From the day after fire, the heliophilous and geophilous species appear in the burned savanna. The attraction is certainly not nourishment, which is still nonexistent.

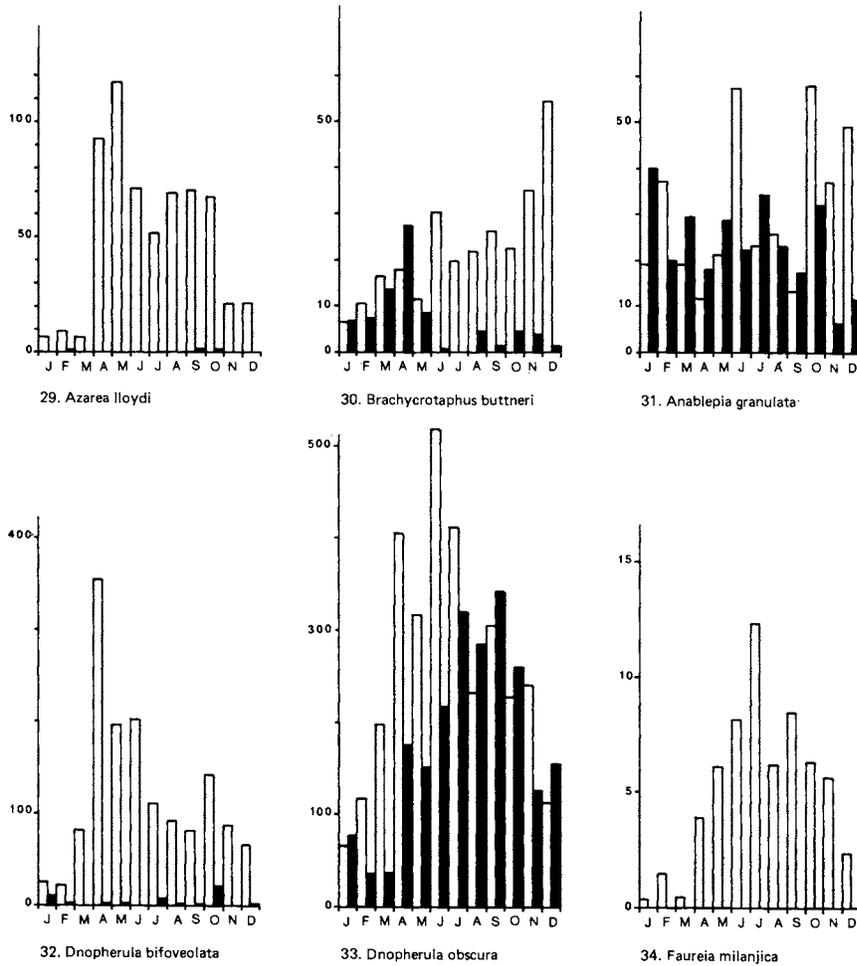
The relative importance of the different herbal species changes for over a month, because the low herbs later choked out by the grasses prosper rapidly (*Cyperus obtusiflorus*, *Brachiaria brachylopha*, *Brachiaria fulva*). The same is true for species with subterranean reserve organs (the grass *Imperata cylindrica*, the composite *Vernonia guineensis*, and many other less abundant species). After the first month, and before the rains, the other grasses grow more than one cm per day, and retake their dominance, such that one finds the specific composition similar to that before the fire. Despite this, the acridid population remains very different from that before burning and from those in the unburned zones. The structures of the two habitats have become very dissimilar. The sun directly reaches large spots of ground between the tufts where, without fire, a thick mattress of dead herbs maintains a constant humidity and shade at the soil level.

The floristic modification which follows when the savanna is spared several years is less radical, and the corresponding acridid species are more linked to humid areas than to particular vegetal species.

Grasse (1929), and Clark (1948) have pointed out this essential role of habitat structure, but we have used fire experimentally to show its importance. In the context of the synecologist, fire is a radical means of modifying the habitat over large areas. Its moment of application, if not its spread, can be controlled. Every other experimental modification of large areas of the habitat (spreading products, plowing, reaping, out of season irrigation) requires major material means.

Dempster (1963), notes two contradictory conditions essential for the success of the acridids: presence of bare soil for egg-laying and vegetal cover for food. Fire offers them bare soil and induces the growth of rich and tender nourishment after eclosion, but it limits

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FIGS. 29-34. Same as Figs. 11-16, additional species.

the food of the maturing adults in the zones where the fire has concentrated them. The mosaic of tufts of grass and bare soil in the first months of growth is certainly favorable to many acridids, but it does not correspond to universally optimum conditions, indicated by the preference of *Rhabdoplea munda* and *Tristria* spp. for unburned zones.

Clark (1967) recognized two habitats for *Chortoicetes terminifera*,

one for oviposition and the newly born, and one sheltering-nourishing habitat for older nymphs and the immature adults. We have not encountered such a phenomenon, but here the habitat is transformed by fire. Recently burned savanna is a good oviposition habitat, and with the growth of vegetation, the sheltering-nourishing habitat develops. After vegetal growth and flowering of the grasses, the sheltering-nourishing habitat is brutally replaced by the oviposition habitat. The development of certain species, be they multivoltine or adults at the moment of this flowering, tends to limit the brood, as does the continued presence, following their initial choice, of the species in the burned or unburned habitats.

In regions where fires occur, their action is such that studies on the repartition and abundance of acridids as a function of other factors, most often botanical (Robertson and Chapman, 1962), should always be accompanied with data on burnings, at least their time of appearance and their spread.

SUMMARY

The monthly comparison by correlation coefficients of rank orders of the acridid population of burned and unburned savanna of the Lamto region of the Ivory Coast permits the study of the transformation of the population from the moment of fire by grouping the data of the most similar months, even though a continuous development occurs as well.

The immediate effects of fire on the population are a marked displacement which generates a gradient of density from the origin of the fire, the burning of certain individuals, and the spectacular predation by raptorial birds.

The structure of the savanna acridid population is described and compared for several periods: in December before the fires, less than 48 hours after the fire, from 1-5 weeks later, at the time of eclosions, and at the end of the year. The populations of unburned zones are also analyzed.

The consequences of the coincidence of fire with various phases of the reproductive cycle of different univoltine and multivoltine species is studied.

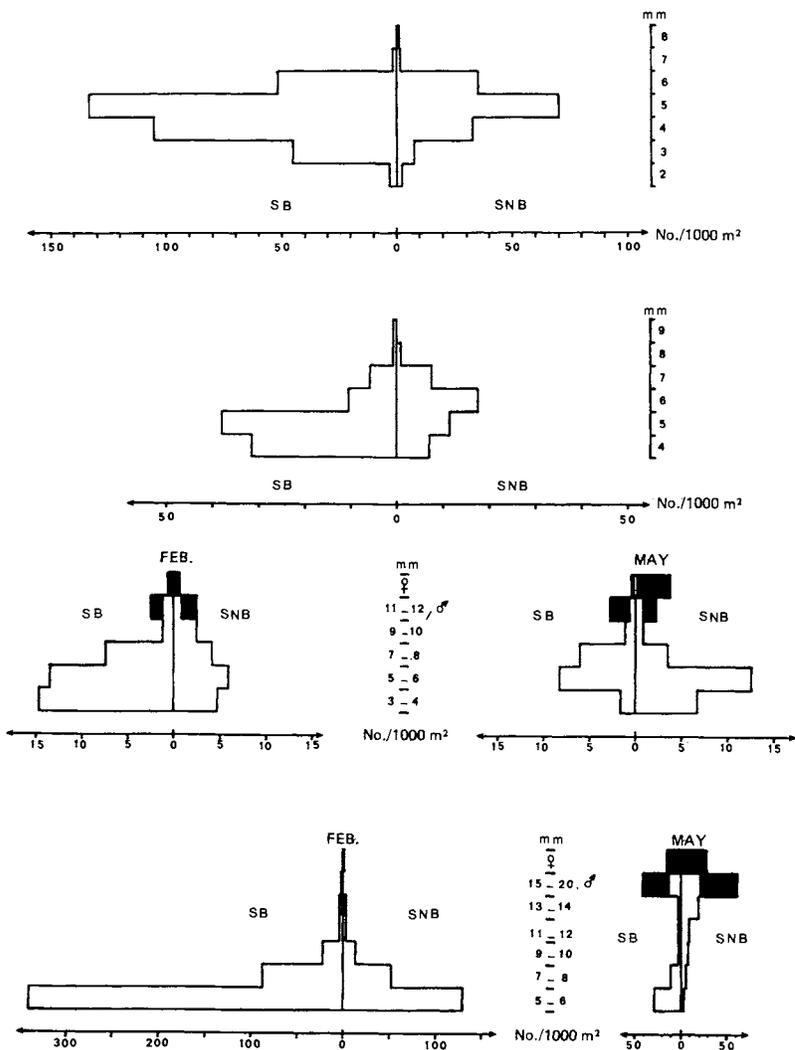


FIG. 35. Comparative structure of the nymph populations of *Dnopherula obscura* in May in burned savanna (SB) and unburned zones (SNB) by size class and length of posterior femora.

FIG. 36. Comparative structure of the nymph populations of *Machaeridia bilineata* in May in burned savanna (SB) and unburned zones (SNB) by size class and length of posterior femora.

FIG. 37. Comparative structure of the nymph populations of *Anablepia granulata* in February and May in burned savanna (SB) and in unburned zones (SNB) by size class and length of posterior femora. The adults are shown in black. Level per 1,000 m².

FIG. 38. Comparative structure of the nymph populations of *Orthochtha brachycnemis* in February and May in burned savanna (SB) and in unburned zones (SNB) by size class and length of posterior femora. The adults are shown in black. Level per 1,000 m².

The comparison of the preceding data with those from a constantly protected parcel suggests several conclusions on the importance of the structure of the habitat to the acridids.

Finally, the reactions of the species to burned and unburned habitats are generally so clear and constant that the most abundant acridids of the savanna could be regrouped according to this criterion.

SYSTEMATIC CLASSIFICATION OF ACRIDIDS MENTIONED

PYRGOMORPHIDAE

- Dictyophorus griseus* (Reiche and Fairmaire 1850)
- Tanita breviceps* (I. Bolivar 1882)

ACRIDIDAE

HEMIACRIDINAE

- Spathosternum pygmaeum* (Karsch 1893)
- Leptacris kraussi* (I. Bolivar 1890)
- Leptacris violacea* (Karny 1907)

TROPIDOPOLINAE

- Tristria discoidalis* (I. Bolivar 1890)
- Tristria marginicosta* (Karsch 1896)
- Petamella prosternalis* (Karny 1907)
- Homoxyrrhopes punctipennis* (Walker 1870)
- Chloroxyrrhopes virescens* (Stal 1873)

COPTACRIDINAE

- Eucoptacra anguliflava* (Karsch 1893)
- Epistaurus succineus* (Krauss 1877)
- Bocagella acutipennis hirsuta* (Kevan 1956)

CALLIPTAMINAE

- Acorypha johnstoni* (Kirby 1902)
- Acorypha karschi* (Martinez 1902)

EYPREPOCNEMIDINAE

- Eyprepocnemis plorans ibandana* (Giglio-Tos 1907)
- Amphiprosopia adjuncta* (Walker 1870)
- Tylotropidius didymus* (Thunberg 1815)
- Tylotropidius patagiatus* (Karsch 1893)

CATANTOPINAE

- Carydana agomena* (Karsch 1896)
- Catantopsilus taeniolatus* (Karsch 1893)
- Catantops* spp.
- Exopropacris modica* (Karsch 1893)

CYRTACANTHACRIDINAE¹

- Acridoderes strenua* (Walker 1870)
- Ornithacris* spp.

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ACRIDINAE

Amphicrenna scalata (Karsch 1896)
Parga cyanoptera Uvarov 1926
Machaeridia bilineata (Stal 1873)
Gelastorhinus africanus (Uvarov 1941)
Cannula gracilis (Burmeister 1838)
Ocnocerus diabolicus (Karsch 1893)
Rhabdoplea munda (Karsch 1893)
Orthochtha bisulcata (Krauss 1877)
Orthochtha brachycnemis (Karsch 1893)
Orthochtha nigricornis (Karsch 1893)
Coryphosima brevicornis (Karsch 1893)
Gymnobotrus linea-alba (J. Bolivar)

OEDIPODINAE²

Heteropternis thoracica (Walker 1870)
Gastrimargus africanus (Saussure 1888)
Gastrimargus procerus (Gerstaecker 1889)
Gastrimargus ochraceus (Sjostedt 1938)

TRUXALINAE

Chromotraxalis liberta (Burr 1902)

GOMPHOCERINAE

Mesopsis abbreviatus (Beauvois 1806)
Mesopsis laticornis (Krauss 1877)
Azarea lloydi (Uvarov 1926)
Brachycrotaphus büttneri (Karsch 1896)
Amesotropis valga (Karsch 1893)
Anablepia granulata (Ramme 1929)
Dnopherula bifoveolata (Karsch 1893)
Dnopherula obscura (Chopard 1947)
Dnopherula sp.
Faureia milanjica (Karsch, 1896)

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¹ *Nomadacris septemfasciata* belongs to this sub-family.

² *Chortoicetes terminifera*, the Australian acridid cited in the literature, belongs to this sub-family.

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