FLUCTUATIONS IN ABUNDANCE OF SOME HOMOPTERA IN A NEOTROPICAL FOREST

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RESUME

Variation de l'abondance de certains Homoptères dans une forêt néotropicale.

La présente note signale les résultats de captures d'Homoptères par piège lumineux dans l'île de Barro Colorado, située dans le canal de Panama. Les Homoptères montrent, comme les autres Insectes, des variations saisonnières considérables de leur abondance. La durée de la période active varie selon l'espèce, mais est en moyenne supérieure à celle d'espèces vivants en zone tempérée, à gels hivernaux. Toutefois les régions tempérées chaudes et les régions subtropicales ne diffèrent pas des tropiques de ce point de vue. Certains groupes animaux, tels que les arthropodes du sol, possèdent des périodes d'activité très semblables à celles des insectes tropicaux. La prédiction de Robinson, selon laquelle une corrélation existerait entre diversité spécifique et coexistence plus soutenue, ne se trouve pas renforcée par les données actuellement disponibles.

L'auteur discute les différences relatives aux types de fluctuation en zones tropicales à saison sèche atténuée et sévère, ainsi que les voies selon lesquelles les insectes peuvent surmonter cette dernière.

Enfin l'auteur définit la variabilité annuelle, composante de la stabilité, comme étant la variance du rapport d'accroissement de l'espèce composante.

En conclusion, les tropiques n'apparaissent pasfondamentalement différents des régions subtropicales et tempérées du point de vue de leur variabilité, ce qui réduit les possibilités de l'hypothèse diversité-stabilité, pour autant que la composante variabilité de la stabilité soit prise en considération.

ABSTRACT

Data are presented on Homoptera obtained by an intensive light-trap sampling program on Barro Colorado Island, Panama Canal Zone.

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These Homoptera show considerable seasonal fluctuations in abundance as do almost all other insect species (from Panama or from elsewhere in the tropics) on which data are available.

The length of the active season varies between species but, on the average is much larger in the tropics than in areas in the temperate zone that do have freezing weather in winter. However, mild temperate and subtropical areas do not seem to be different from the tropics in this respect. Animals such as soil arthropods, that are to some extent sheltered from the cold, have active seasons very similar to those of tropical insects. The available facts do not support the prediction by ROBINSON *et al.* (1974) that there should be a correlation between a more sustained coexistence and species diversity. Also, there is no evidence suggesting that closely related sympatric species stagger their active season as adults in order to avoid competition.

Differences in fluctuation patterns between tropical areas with a mild and with a severe dry season are discussed and so are ways in which insects may cope with the dry season.

As a component of stability the author defined annual variability as the variance of the rates of increase of the component species. The tropics do not seem to be different from subtropical or temperate areas in their variability, leaving thus very little room for the diversity–stability hypothesis as far as the variability component of stability is concerned.

INTRODUCTION

In recent years a controversy has developed about stability of complex ecosystems such as a tropical forest. A notion that a diverse fauna and flora results in a large stability gained wide acceptance and became known as the diversity–stability hypothesis. FUTUYMA (1973) expressed some doubts about it. GOODMAN (1974) has reviewed the evidence brought forward to support the hypothesis. He concludes that this evidence is very shaky, to say the least, and he questions the very existence of a community property that could meaningfully be called stability. MAY (1973) concludes that there is no mathematical argument supportting the hypothesis and, in fact, for his model ecosystems, finds that diversity tend to produce instability. DE ANGELIS (1975) finds that in such models, in some circumstances, diversity can produce a greater stability. Part of the problem is the meaning of the term "stability." ORIANS (1974) lists a number of concepts that are hidden behind the term stability. One of these concepts he calls constancy, which is defined as a lack of change. However, I suggest that it is more practical to call it "variability", to be defined as the amount of change. This would reduce to constancy only if the amount of change is nil, which may never happen. The amount of change within a year is the seasonal variability, the change between years is the annual variability. I will concentrate on the latter in the present paper. For individual species the annual variability is measured by the

rate of increase (R), which is simply the number of individuals in a given year divided by that in the previous year. For an ecosystem, or part of an ecosystem, it can be depicted by the frequency distribution of the rates of increase of the component species. On a logarithmic scale this distribution is approximately normal. Annual variability is measured mainly by the variance of this distribution and, to a much lesser extent, by its mean. The mean of log R is the logarithm of the geometric mean of R and measures general increase or decrease of the fauna as a whole. The variance of log R measures differences between species in their rate of increase with resulting changes in the relative abundance of these species. For the moment I will define variability as the variance of the distribution of the (log) rates of increase, keeping in mind that a mean rates of increase different from zero should be taken into account when comparing ecosystems or geographical areas.

There is reason to suspect that species having a more complicated web of interactions with other organisms fluctuate less (DEN BOER, 1968, 1971; REDDINGIUS and DEN BOER, 1970). Then, if presence of a larger number of species is an indication of a more complex interaction web (this is not necessarily so), a system such as a tropical forest should have a lower variability and thus be more stable in the above sense than simpler systems such as obtain in the temperature zone.

Almost all of the arguments in the literature pertaining to the relative stability of tropical forest are theoretical. Many of the points are well taken and persuasive, but it is just possible that they are wrong. Nature may not feel itself limited by our lack of imagination.

In the present paper I will discuss some data on a large number of species of Homoptera. These data are fairly crude, but show rather convincingly and perhaps surprisingly, that the estimated annual variability in a tropical forest is the same as that found in temperate areas. This undoubtedly highly complex system with a very large richness of species is just as variable, or stable, as other systems that are much more simple.

PROCEDURES

The data to be discussed were obtained in a tropical lowland monsoon forest on Barro Colorado Island (BCI), Panama Canal Zone, During the rainy season, from May until December, rainfall averages 30 cm per month. During the dry season, wich is rather severe, it averages some 6 cm per month (Figure 1, taken from SMYTHE, 1974). There is a considerable variation in rainfall pattern from year to year and this variation, especially during the dry season (Figure 2), may have important consequences, as will be discussed later. Temperature does not vary much. The daily fluctuations in temperature average from 22.6° to 31.4° C just outside the forest and from 22.1° to 28.0° C in the forest, near the forest floor. In the canopy, daily fluctuations in temperature may be somewhat higher with a higher average (SMYTHE, 1974; ALLEE, 1926). Relative humidity in the forest
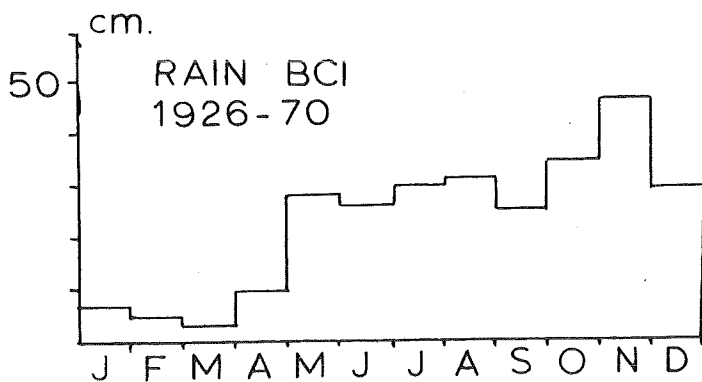
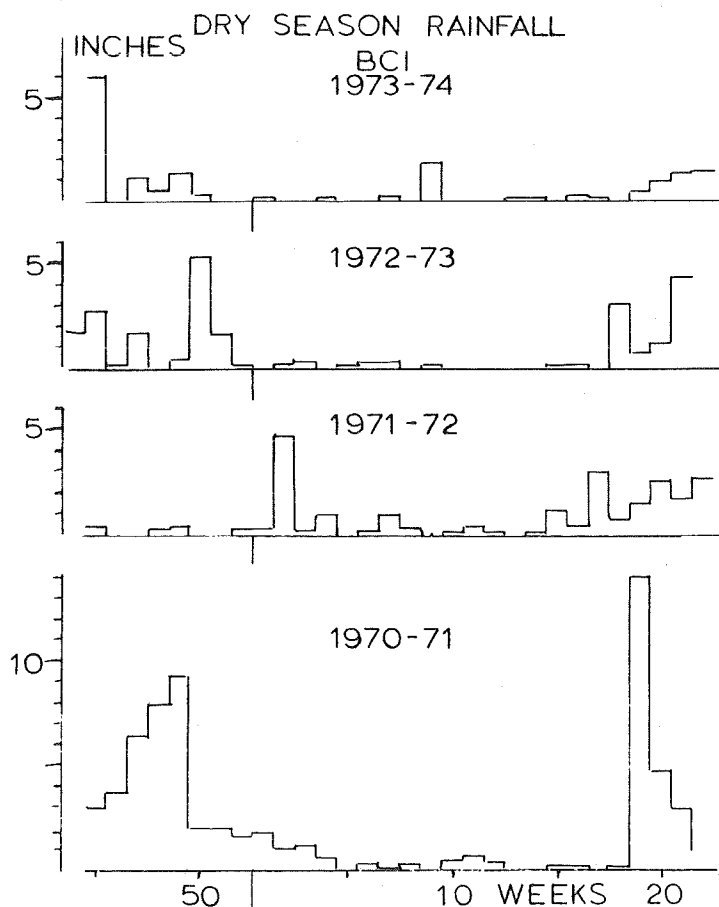*Figure 1* : Mean monthly rainfall in cm on Barro Colorado Island. (Smythe, 1974)

Figure 2 : Rainfall per week, in inches, for 4 successive dry seasons on Barro Colorado Island.

varies between 76 °/o in April to 94 °/o in November, near the forest floor (SMY-THE, 1974). GIBBS and LESTON (1970) subdivided their rainy and dry seasons in Ghana in sunny and dull seasons. With the available analysis of climatic data I see no reason to do so for Panama, except perhaps that the very end of the dry season (which is mostly sunny) could be called dry–dull.

The insects are collected with two sets of light–traps in the forest and one trap in more open country in Las Cumbres, some 16 kilometers north of Panama City, Republic of Panama. The former were set up by Smythe as part of the Environmental Science Program of the Smithsonian Institution. For details about the traps see SMYTHE (in preparation). One set of three traps was installed in 1971 in a valley at the *weir*. The other set of two traps was installed in the beginning of June 1973 on a ridge at *Snyder–Molino 3* (S-M, Figure 3). Each set has one
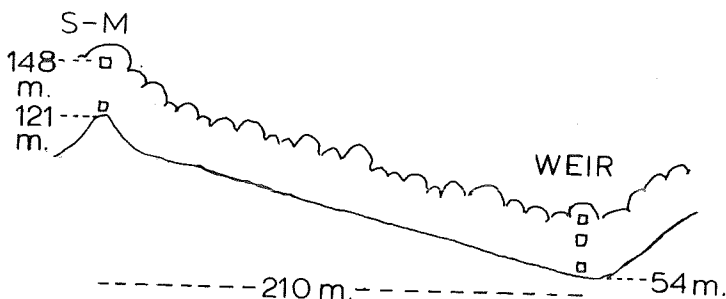

Figure 3 : Location of the light–traps at Snyder–Molino-3 (S-M) and at the weir, with the altitudes above sea level.

trap at some 27 meters high in the canopy and one near ground level. The weir set has also one trap at an intermediate level. The weir traps yield one collection per week and are operated for four consecutive nights, for two hours per night. The S-M traps operate all night and, until recently, yielded five collections per week, four daily samples and one weekend sample. Since early December 1974, they have provided seven daily samples per week. The trap at Las Cumbres was given to me by Smythe and is situated behind a house overlooking a valley with a variety of ornamental, fruit, and wild trees and shrubs and some open areas. This trap is in operation since October 1973 and produces seven samples per week.

Because in the present paper I am concerned with the forest, the data from Las Cumbres will be mentioned only occasionally; so will the data from the weir traps as generally they produce not enough insects to permit a meanningful analysis at the species level.

The entomofauna of BCI is very rich and for practical reasons I have to restrict myself to one group, which is sufficiently rich in species, which appears commonly in the traps and which at the same time is not too difficult to handle taxonomically. I selected the Homoptera. Some other groups of insects are also being sorted by specialists in those groups. In the present paper I will restrict myself to those species of homopterans for which I am reasonably sure that they are indeed good species and for which the data have been analysed. Groups for which the data have not yet been analysed include Membracidae and Typhlocybinae (Cicadellidae).

RESULTS

Before presenting the data, some discussion is necessary about their quality. Light–traps attract only insects that can fly, that fly at night, that are attracted to the lights, that manage to fall down the funnel into the cloth bag, and that are unable to climb out again before they are killed by the carbon tetrachloride. There are large differences between species in the probability to get caught. Several species of homopterans that I see frequently in the understory of the forest hardly ever show up in the traps. The data, therefore, do not give much information about the relative abundance of species. Because most, if not all, species (even the diurnal ones) do eventually appear in the traps, an estimate of species richness (that is, the number of species present; HURLBERT, 1971) can be obtained. No information, however, is available to calculate the evenness–component of species diversity of the homopteran fauna.

The capture probability of some species may change within a season. Species that are partly noctural early in the season may become completely diurnal later on. Gravid females may be unable to fly and entire generations within a season may not fly (WALOFF, 1973; ROSE, 1972 a, 1972 b). Such complications probably do not occur with most of the species I am dealing with; but, unless one is sure that they don't, extreme care should be taken in interpreting the observed fluctuation patterns in the captures.

Moonlight, rain, wind speed, etc., may affect the probability that individuals of any given species are being caught, resulting in sometimes rather wide fluctuations from day to day. A sampling program with only one sample per week or so might yield samples too variable in the numbers caught to be useful as an indication of changes in abundance in the area. A much more intensive sampling program, such as the one at S–M and Las Cumbres, tends to even out effects of vagaries of the weather and show the effect of the moon clearly enough to take it into account.

I submit that the data obtained with our sampling program do give an indication of the actual seasonal and annual changes in abundance of the adults in the populations, at least for most species. And even if, in some species, part of the generations or even entire generations within a year are not being caught

or are being captured at a smaller rate than at some other time of the year, between-year comparisons should still be valid. Pitfall traps are light-traps in that one can think of all sorts of reasons why the data obtained could be suspect. Nevertheless, DEN BOER (1971) has shown that they do give rather good estimates of rates of increase of Carabid beetles.

The Seasonal Pattern

The general abundance per week, in the S-M traps, of some major groups of homopterans is given in Figure 4. The family Delphacidae is treated separately from the rest of the Fulgoroidea because they seem to behave rather differently.
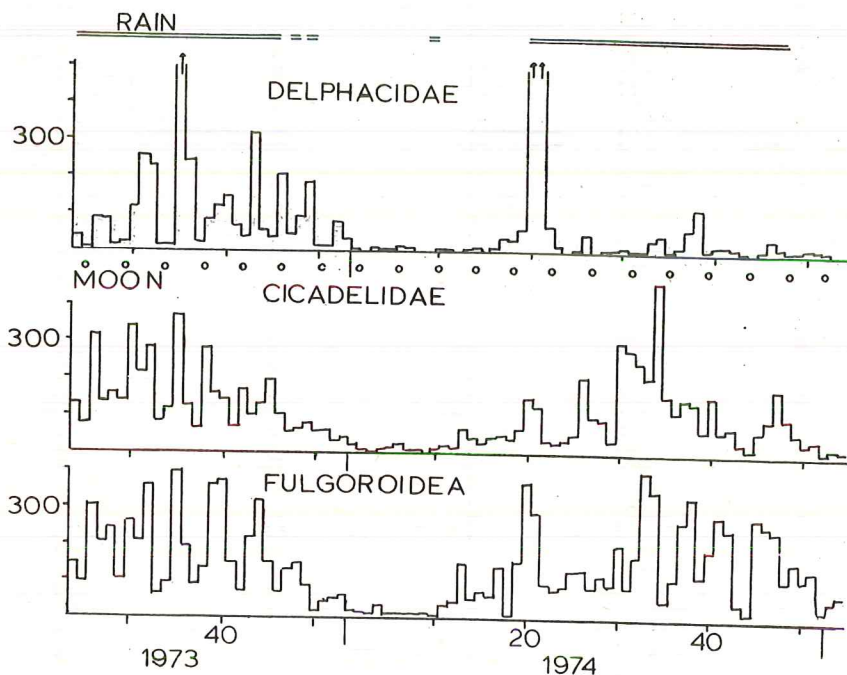

Figure 4 : General fluctuation in abundance of three major groups of Homoptera in the traps at S-M. The double fine at the top indicates period with rain, the series of circles indicates the times of the full moon.

Individual species show large variations from day to day. They have, from time to time, major flights whenever large numbers of alate forms are available and the weather pattern is right. Such flights may last only one night. Such erratic patterns are not obvious in any of the other groups.

The effect of the full moon is striking, especially in the fulgoroids, where there is an up to sixfold difference between weeks with and without full moon.

This moon effect is not equally apparent in all species. For instance, in *Ambly-cratus fuscolineatus* (Achilidae) (Figure 5C), it is very strong although less so in October–November, while in ˇAchilid sp. 51B˝ (figure 5A) it is almost absent.
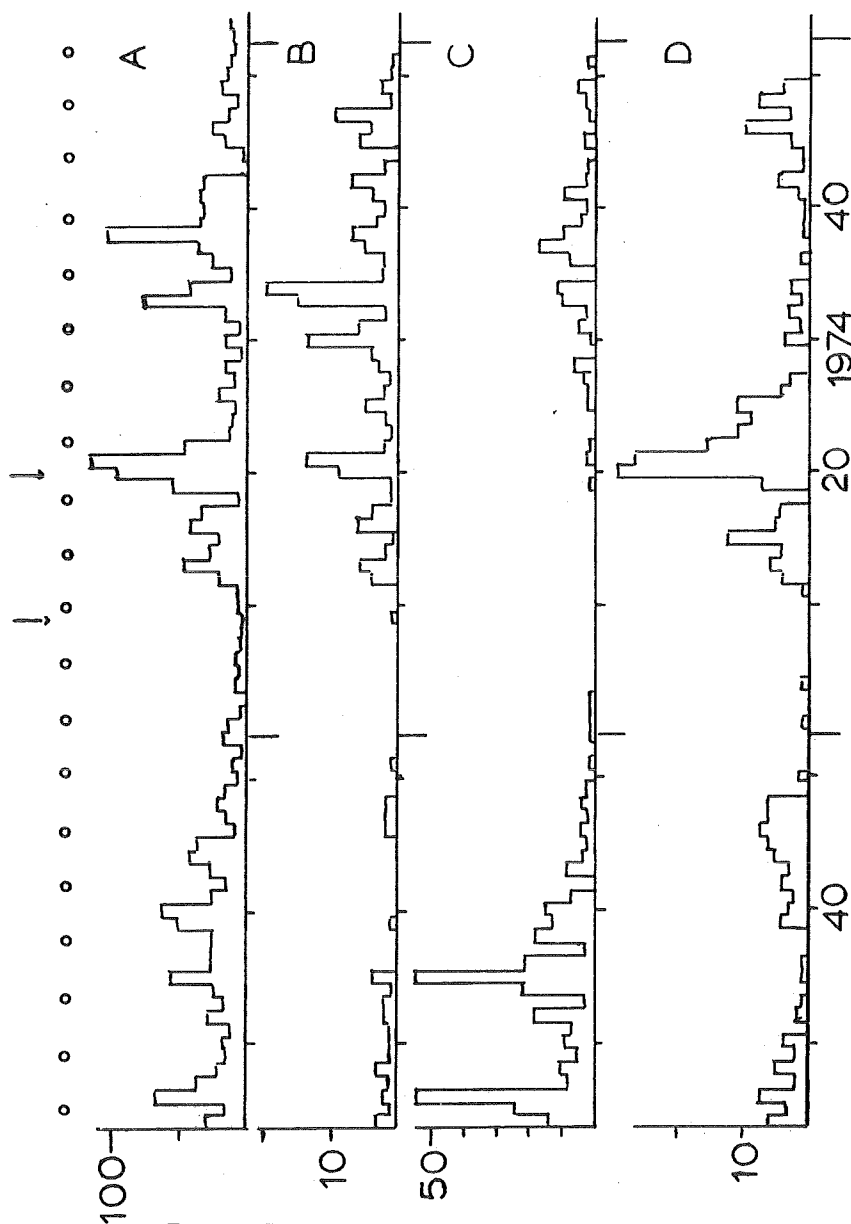

Figure 5 : Fluctuation pattern of 4 species of Fulgoroidea.
A : Achilidae sp. 51B (looks like a small Catonia, but is not).
B : Anormenis nigrolimbata (Flatidae).
C : Amblycratus fuscolineatus (Achilidae).
D : Muirolonia metallica (Cixiidae).
The two arrows at the top indicate the mid dry season rainfall and the beginning of the rainy season respectively. The circles are the times of full moon.

During the dry season many fewer individuals and fewer species are caught than in the rainy season (Figure 6). The difference in the number of individuals (100–fold) being much larger than that in the number of species (tenfold), which is in agreement with the results found by JANZEN (1973). This means that not only is the number of species reduced but also that the species that remain present have fewer individuals. Figure 6 needs some explanation. It contains only data on those species for which we are reasonably sure that they are indeed one species.
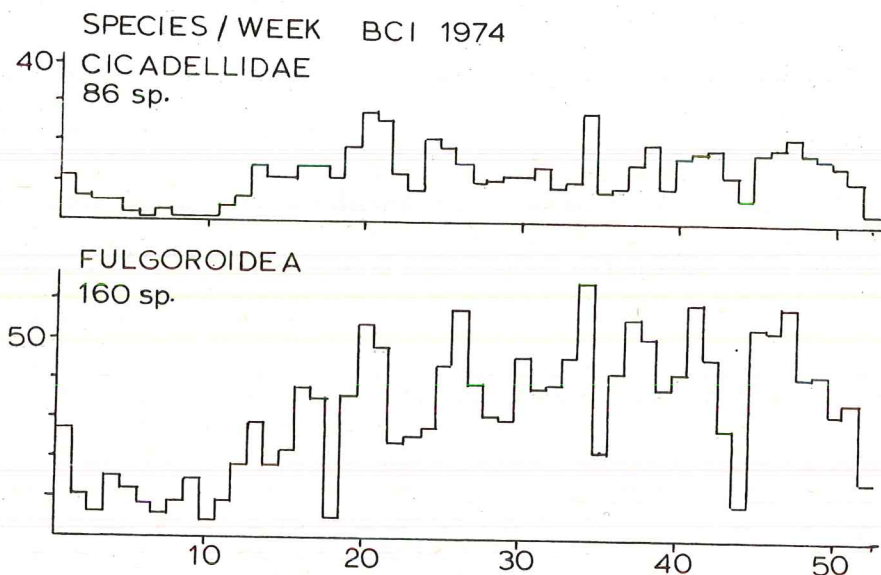

Figure 6 : The number of species caught per week of Cicadellidae and Fulgoroidea. All groups for which we have not yet been able to separate the species in a satisfactory way are not included.

Several genera contain groups of species that look very much alike and that we have not yet adequately dealt with. Such groups, including the entire subfamily of the Typhlocybinae, are not included in Figure 6, although the individuals are included in Figure 5. The reduction of numbers in the dry season is confirmed by visual observations and sweeping in the forest. JANZEN (1973) observed the same phenomenon in his extensive sweeping program and it is definitely not an artefact produced by the light–traps not operating properly in the dry season. Such explanation *a priori* should not be ruled out. The higher wind speeds during the dry season could conceivably adversely affect the numbers of insects caught. However, the few days in the rainy season with rather high wind velocities, and the days during the dry with relatively low wind speed, were not in any way different from normal days in the same period.

An interesting clue to what is going on is provided by the heavy rains during the first week of March, right in the middle of the dry season in 1974 (Figure 2). It was followed by some ten weeks of dry weather. Soon after this "unusual" rain (it happened again in 1975 !), the number of individuals and species increased. This phenomenon can best be appreciated by looking at individual species, exemplified in Figure 5, where it is present in three of the four species shown. In some species (not shown) where there was a clear–cut separation of generations in 1973, this was not so in 1974. The 1973 dry season was dry throughout. Unfortunately I do not have insect data for that year until early June. The interpretation is that many species aestivate as nymphs. In some species, some nymphs in wetter spots may continue to develop and produce some adults throughout the season (Figure 5A). The rains in week 9 caused the aestivating nymphs to develop and several reached the adult stage. These are the ones that appeared in the traps after the time lag of some 3–5 weeks. This delayed response suggests that the species is not aestivating as adults. Other nymphs found themselves in dry conditions again and started another period of aestivation, but at a much more advanced stage of development. These responded to the next rains in week 20 (mid–May) by emerging as adults almost immediately, without an obvious time lag. Several species that did respond to the first rain in March seem to be doing fine during the dry weather. There is no indication that they died off more rapidly than during the rainy season and the fluctuation pattern later on suggests that they also successfully reproduced. Why, then, are such species, that apparently can survive and multiply successfully during dry weather conditions, normally absent or at low densities during the dry season ? The answer probably lies in the fact that much of the vegetation also responds to rain, even if this rain is in the middle of the dry season. This response consists of a flush of new leaves and shoots which normally does not appear until May. The insects can take advantage of this resource even though the weather is still dry. Other species may not do so well. Some, that were absent or almost absent during the first half of the dry season, produced one or two individuals for the traps after the mid dry season rains and then disappeared again. Others showed no response in the traps at all (Figure 5C), but started appearing immediately when the rains really started in May. I assume that at least some of these species also aestivate as nymphs, that they also continue their development after the rains in March, but that the emerging adults fail to survive and multiply. Either they cannot cope with the dry conditions or their foodplant does not produce new leaves and shoots.

JANZEN and SCHOENER (1968) suggest that many insects in seasonal tropical forest may pass the dry season as active adults in reproductive diapauze, taking advantage of whatever humid refugia are available. This is certainly true for some open country cicadellids that feed on grasses and other plants in grasslands. The parts of these plants above the ground die off completely during the dry season, leaving food for the insects only in sporadic humid spots. In such spots I have collected large numbers of, for instance, *Plesiommata mollicella* and *Agallia modesta* without finding any larvae. For the forest homopterans I have very little data that suggest that this phenomenon occurs there. It may be true, however,

for the achilid *Plectoderes* ` sp. 58B ´ (possibly *P. collaris*). During the dry season this species was caught exclusively in the traps at the weir, in a valley, near a creek, an area more humid than either S–M or Las Cumbres where they were only found during the rainy season (Figure 7). I have yet no information on the reproductive condition of these insects during the dry season.
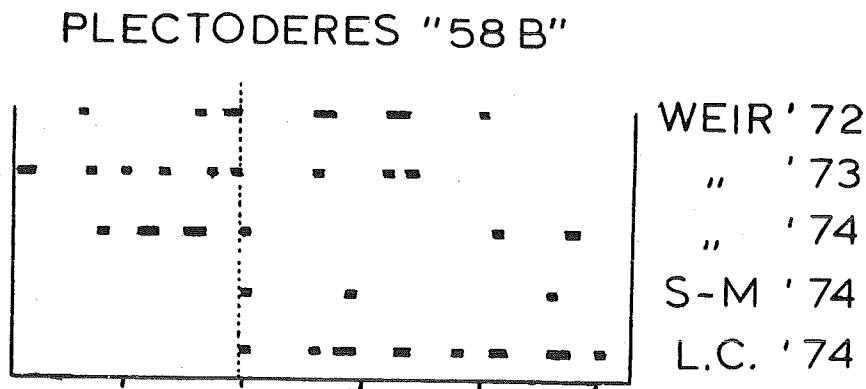
PLECTODERES "58 B"

WEIR ' 72

„ '73

„ '74

S–M '74

L.C. '74

Figure 7 : Presence in three kinds of traps, the two sets in the forest and the trap in Las Cumbres, outside the forest, of the species Plectoderes sp. 58B (Achilidae), showing that during the dry season it is only found in a relatively humid area at the weir.

As JANZEN (1973) points out, the dry season is not necessarily inimical to all insect species. Of the forest cicadas of which I have some information (Figure 8), three were restricted to the dry season (*Dorisiana viridis, Pacarina puella* and *Selymbria* ` sp. H2 ´). The first and second of these also occur in open country where they are together with at least two other species of cicadas (*Quesada gigas* and an unknown species, probably *Quesada* sp.) both restricted to the dry season. Apart from these cicadas, however, none of the many other species of homopterans are restricted to the dry season, nor does there seem to be a single one which has a peak in abundance during the dry season. Apparently none of these species has been able to evolve an adaptation to dry season conditions, thus taking advantage of the relatively low abundance of predators and / or competitors.

Some species caught in the traps in the forest obviously are not living there, or live only at some isolated grassy sunny spots. Their major distribution is in open grasslands. Such species characteristically appear only during two periods of the year. The first is in May when the rains start, the second at the end of the year. At both times there is a major flight activity in the open areas, such as in Las Cumbres, either to find the newly available resources in May or to find moist refugia at the beginning of the dry season. Figure 9 gives, as examples, the data for *Plesiommata mollicella* (9A) and *Tylozygus geometricus* (9B). The latter species builds up its numbers in Las Cumbres during the rainy season, reaching a first
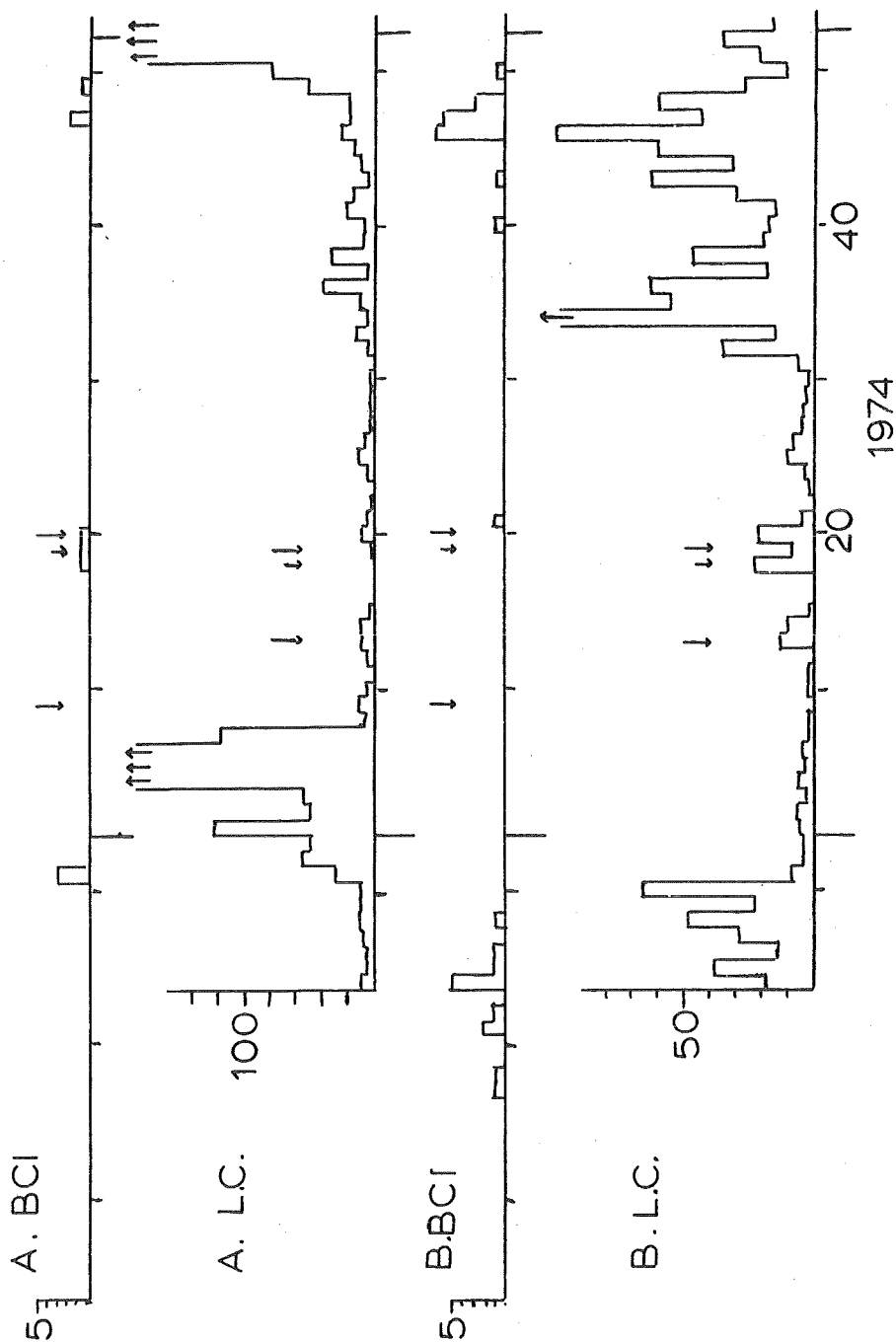
Figure 9 : The occurrence in the traps in the forest on Barro Colorado Island and in open areas (Las Cumbres) of two species of grassland Cicadellinae, viz. Plesiommata mollicella (A) an Tylozygus geometricus (B). In the forest they are classified as seasonal migrants.

CICADAS BCI 1974

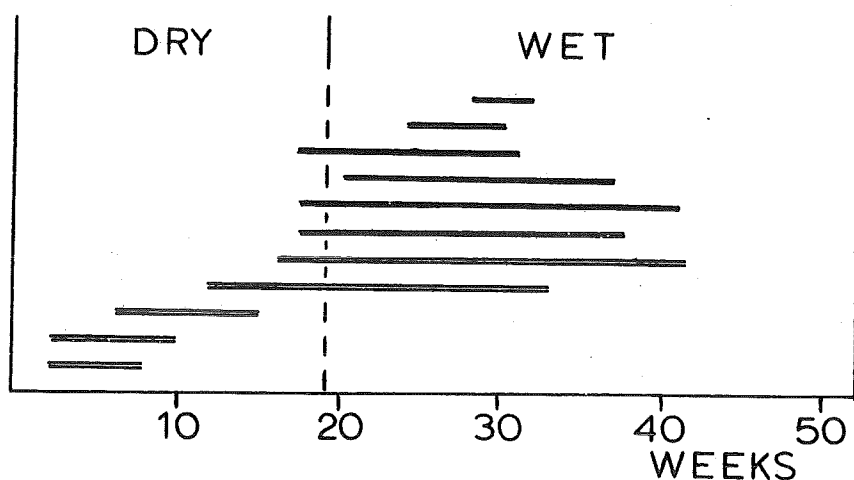
Figure 8 : Seasonal occurence of forest cicadas, showing that there are three dry season species.

peak by the end of August. A second peak occurs by mid–November, which seems a bit early to explain a dispersal peak during dry weather. Nevertheless, this peak coincides with the appearance in the traps in the forest. *Plesiommata mollicella* shows basically the same pattern except that the larger trap abundance in Las Cumbres at the end of the year is definitely correlated with a deterioration of their environment. In 1975 the dry season started earlier and the grass turned brown earlier than in the 1974. The enormous peak in the traps (of up to 1700 per week) correlated with the dying off of the grasses in the lawns and roadsides. Strangely enough, the appearance in the forest traps was much earlier, late November and early December. The same phenomenon, much clearer, was found in *Tylozygus fasciatus*, where a major appearance in the forest traps preceeded the Las Cumbres flight peak by several weeks. Of course, one would not except the correlation to be perfect. The individuals in the forest come from open area, but very likely not from Las Cumbres, which is some 34 kilometers away. Rainfall is very patchily distributed and the areas where these migrants do come from just might start drying out earlier. However, I don't think that this is very likely for two consecutive years. It seems much more probable that these insects use some proximal clue other than the weather to escape from the dry conditions well before these arrive. Seasonal dispersal also occurs in forest insects. Figure 10 gives an example of a cicadelline "sp. 155", a forest species that appears in the traps in Las Cumbres early in the season and towards the end of the year. Here the time of dispersal coincides with a decrease in the forest. In such cases, where the normal habitat of a species is known, it is not too difficult ot recognize them as migrants, seasonal or otherwise. Other cases are more difficult. Figure 11 gives the fluctuations of
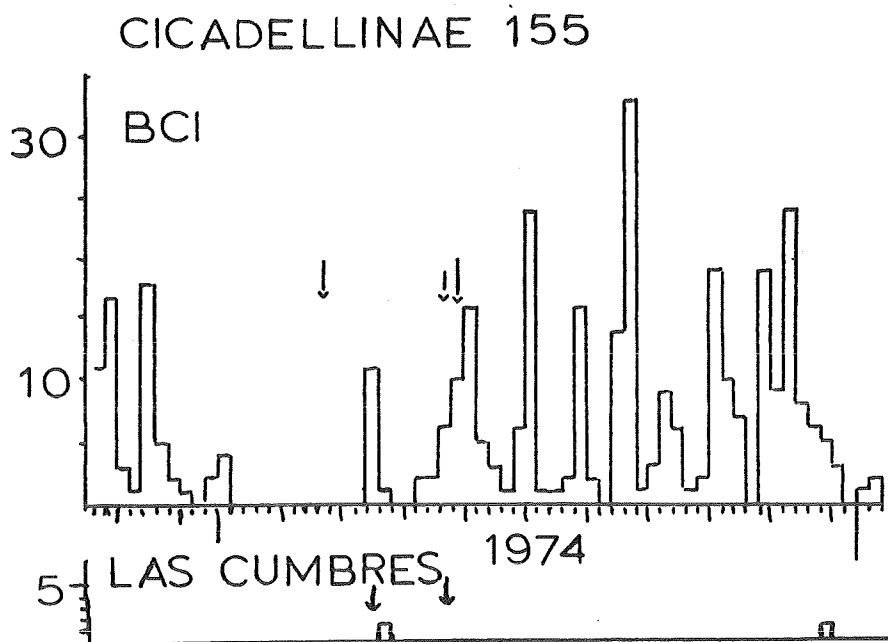
Figure 10 : Occurrence in the traps of a forest species (Cicadellinae 155) which, in open areas, is classifed as a seasonal migrant.
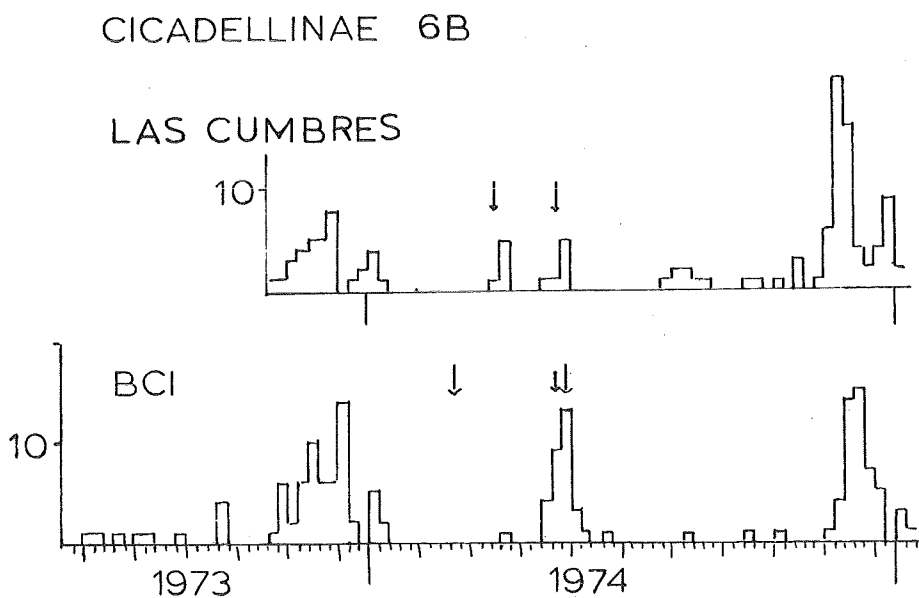

Figure 11 : Seasonal fluctuation of a species (Cicadellinae 6B) with two well-defined peaks of abundance per year, one at the beginning and one at the end of the rainy season, both in open country and in the forest.

a cicadelline ``sp. 6B´´ which appears in the traps clearly both at the beginning
and the end of the rainy season, with only occasional captures in between, both
in Las Cumbres and in the forest. It could be a seasonal migrant, but I doubt
that. I rather suspect that this is a species which flies little or turns completely
diurnal in the rainy season between the peaks in the traps. Anyhow, the light-
trap data alone on such species are of doubtful value for determining presence
or absence in the forest and the length of their active season.

For the adults of many species, however, it was possible to define the active
season in the forest and its length. The data give underestimates because by the
beginning and the end of the season, when numbers are low, the numbers caught
could easily be zero although the species was already or still present. For cicadas,
the actual active season, as determined by monitoring their calls, usually was
somewhat longer on both ends than shown by the light-traps. Data on species
that were obtained in sufficiently large numbers are presented in the top graph
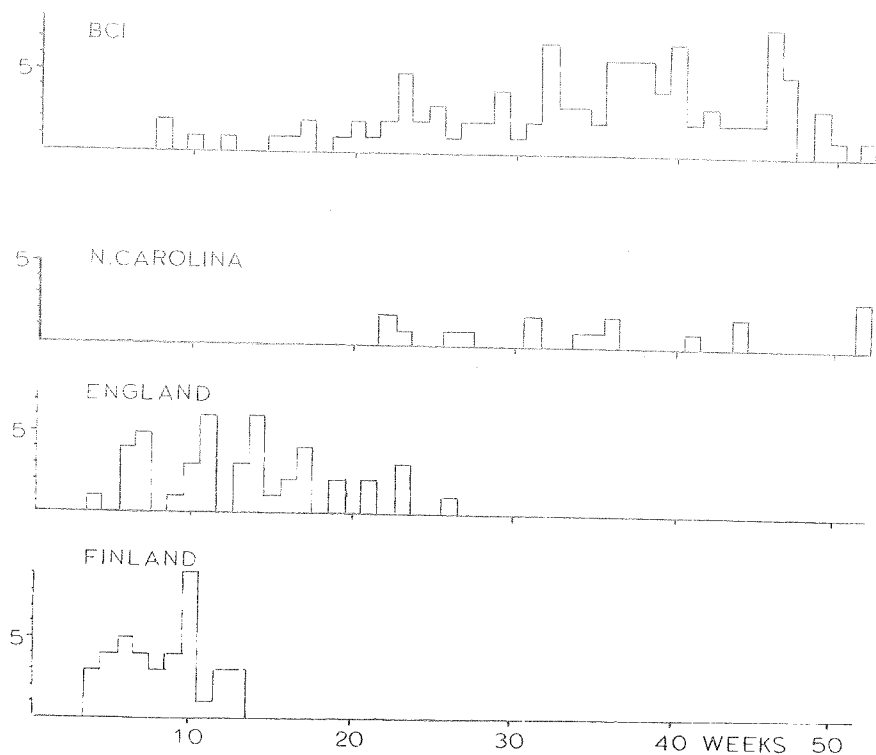of Figure 12. This figure shows a wide scattering of the species. Some were present

Figure 12 : Distribution of the length of the active season of Homoptera in the forest on Barro
Colorado Island, in salt marshes in North Carolina (Davis and Gray, 1966), and in grasslands
in England (Waloff, 1973) and in Finland (Kontkanen, 1950).

only for a period of eight consecutive weeks per year, others were present through most of the year in the traps and, in the forest, may have been present year round. The important point is that some species occur only during a short period of the year. The achilid *Myconus uniformis*, for exemple, occurred for a period of 12 weeks in 1974 in Las Cumbres and also, during the same weeks, in 1974 and 1973 in the forest. More data might shift the general distribution of the data in Figure 5 (BCI) somewhat to the right, but several species will remain in the far left–hand part of the graph. Mean length of the active season is 34.2 weeks.

As one might have expected, the seasons of homopterans in places like England (where there is a cold winter) are much shorter, on the average (Figure 12). In Finland, with a much longer and colder winter, the season is shorter still. However, in North Carolina, USA, in salt marshes (DAVIS and GRAY, 1966), with a climate that is classified as ``humid subtropical´´, both mean and variance of season length of homopterans are almost identical to those obtained from the tropical forest on BCI.

Variation Between Years

The data from the traps at the weir that have been is operation for over three years is shown. Unfortunately, the data are not good enough (for most species) to permit analysis of changes in abundance between years. However, for some species, individuals were obtained in sufficient quantity. The data are presented in Table 1. There are only seven species for which a rate of increase (ratio of the abundance in two consecutive years) could be calculated and the data are considered insufficient to calculate a meaningfull annual variability as defined above.

TABLE 1

Between–year variation in abundance in light–traps of some Homoptera in the forest on Barro Colorado Island (Panama Canal Zone). Weir traps.

	1972	1973	1974	73/72	74/73
FULGORIDAE					
Calyptoproctus elegans Oliv.	18	29	16	1.61	0.55
CERCOPOIDAE					
Tomaspis sp. 52A	29	41	62	1.41	1.51
Microsargane vittata Fowl.	15	22	11	1.47	0.50
ACHILIDAE					
Plectoderes sp. 58B	20	15	16	0.75	1.07
CICADOIDEA					
Dorisiana panamensis Davis	5	2	1		
Taphura sp. C	74	104	63	1.41	0.61
Fidicina mannifera Fab.	24	10	18	0.42	1.80
Pacarina puella Davis	10	9	6	0.90	0.67
Dorisiana viridis Oliv.	4	–	2		
Selymbria sp. I	5	4	1		

The S-M traps produced much better data. They started collecting insects early in June 1973, so that I do not have two entire years to compare. Such information will become available, but it is highly instructive to compare the last seven months of 1973 with those of 1974. This covers only 56 percent of the time, but a much higher percentage of the individuals, because the five months excluded include the entire dry season, when the numbers are low. In 1974, 75 percent fo the fulgoroids and 82 percent of the cicadellids were caught in the seven months from early June until the end of December. Taking only those species that, at least in one of the two periods, produced more than ten individuals in the traps, there are 110 species that can be used at this moment. The data are presented per (sub)family in Table 2. The number of species per (sub)family usually are

TABLE 2

Between-year changes in abundance of Homoptera in light-traps in the forest on Barro Colorado Island. Snyder-Molino traps. Compared are the period of 6 June to 31 December 1973 with the same period in 1974. Only species with more than 10 individuals in at least one of the years are included.
R = ratio 1974/1973.

Group	Number of species	log. R	
		Mean	Variance
FULGOROIDAE			
Achilidae	20	0.0388	0.1290
Cixiidae	13	-0.1431	0.4476
Flatidae	13	0.4781	0.0990
Dictyopharidae; Fulgoridae	5	0.3843	0.0993
Tropiduchidae; Kinnaridae	2	0.2465	0.0644
Derbidae	9	-0.1775	0.1163
Delphacidae	12	-0.7304	0.1702
TOTAL FULGOROIDEA	74	-0.0381	0.3148
CICADELLIDAE			
Cicadellinae	10	-0.2114	0.1089
Xestocephalinae	2	0.3956	0.0179
Idiocerinae	4	-0.4901	0.1819
Gyponinae	1	1.3222	
Deltocephalinae	6	-0.4001	0.1401
CERCOPOIDEA	4	0.3718	0.1644
PSYLLIDAE	5	0.1154	1.8627
TOTAL	110	-0.0479	0.3506

TABLE 3 : Annual variability in some tropical, subtropical, and temperate insects. N = number of species; R = ratio of abundance in two consecutive years; * = data used in Figure 13.

Author	Group	Locality	Year	N	log R Mean	log R Variance
Clarke, 1968	Tabanidae	Zambia	1963-64	17	0.4479	0.2272
Rothschild, 1970	Pyralidae	Sarawak	1965-66	5	0.4151	0.1944
Galindo et al., 1956	Mosquitoes	Panama	1949-54	15	0.0346	0.2415
Present paper	Homoptera	Panama	1973-74*	110	-0.0479	0.3506
Hughes et al., 1965	Aphids	Australia	1961-62			
		Gordonvale		5	-0.0284	0.1298
		Brandon		8	-0.0680	0.1760
		Mackay		7	-0.3531	0.1693
		Bundaberg		6	-0.4487	0.6201
		Rydalmere		26	0.4020	0.2699
		Merbein		5	-1.3530	0.1978
		Adelaide, Waite		14	0.1767	0.4804
		Adelaide, Hills		13	0.1069	0.4748
		Canberra		20	0.3104	0.1129
		Burnley		26	-0.1748	0.1796
		New Town		33	-0.0854	0.2186
		Grove		17	0.0480	0.1215
Williams, 1939	Lepidoptera	England	1933-34*	119	-0.0124	0.2884
		England	1935-36*	114	-0.6199	0.2268
Best, 1950	Lepidoptera	England	1948-49	22	0.0240	0.1530
Dirks, 1937	Lepidoptera	Maine, USA	1932-33	64	0.1859	0.2189
Crichton, 1960	Trichoptera	England	1953-54	38	0.2180	0.4768
New, 1970	Psocoptera	England	1966-67	8	0.1446	0.3471
Waloff, 1973	Homoptera	England	1970-71*	3	-0.1208	0.0313
Waloff & Solomon, 1973	Homoptera	England	1969-70*	7	-0.0721	0.0342
Park et al., 1973	Pselaphidae	Illinois, USA	1968-69*	15	0.2914	0.2593
McFadyen, 1952	Soil arthropods	England	1948-49	5	0.1211	0.1196
v.d. Drift, 1959	Carabidae	Netherlands	VIII 50 - 51	67	0.0026	0.3313
			1950-51*	22	0.1084	0.2608
			1952-53*	17	-0.3492	0.2150
Kontkanen, 1950	Homoptera	Finland	1954-55*	11	0.0530	0.3461
			1947-48*	35	-0.0398	0.1116

small so that not too much confidence can be given to differences between the groups in the variability shown in the last column in the table. Some of the differences could very well be real. All flatids and all dictyopharids increased in numbers from 1973 to 1974, producing a large positive mean (log) rate of increase, while almost all derbids and delphacids decreased. The more important figure at the moment is the total variance for all 110 species, which is 0.3506. This measures, by definition, the degree of variability (stability) of this particular Neotropical forest, in these particular years, as far as the homopteran component of the fauna is concerned. This variance of 0.3506 means that the 95 percent interval of R is from 0.059 to 13.4. Data on species of other groups of insects from BCI are not yet available, but my impression thus far is that they probably also have a variability similar to the one obtained with the homoptera.

For comparing these data with similar data from the cold–temperate zone and from other tropical areas, I certainly have not yet exhausted the literature. Some data that I have obtained thus far are presented in Table 3. The results depend on the accuracy of the techniques used. The sampling error component of the variance will be smaller, the more accurate the estimates are. The significantly lower variability of Kontkanen's homoptera in Finland as compared with that of those from Panama could simply mean that his sweeping technique produced more accurate results. Most of the data in Table 3 are obtained with light–traps, pitfall traps, Moericke traps, suction traps, etc., meaning that they may have a comparable sampling error. The general picture that emerges is that the tropical data do not stand out in any way. There is nothing special about fluctuations of insects in the tropics, even in a tropical forest. The variability of tropical insects is just about the same as that of other insects found in other parts of the world. The actual frequency distributions of log R for some of these data (Figure 13) show this even more clearly.

For most of the species, data on their life history, food plants and enemies are completely lacking. In fact, many of them are even unknown taxonomically. Any attempt, therefore, to try to explain why some species increased and others decreased in abundance from 1973 to 1974, or why some species are present only for a short period during the year while others are present year round, has to be treated with great caution. However, the available data do suggest that variation in the rainfall pattern is a factor that could be important for at least some species. As has already been discussed, some species responded clearly to the rains in the middle of the dry season by an increase in abundance in the traps; others showed only a weak response and still others did not appear at all in the traps after those rains (Figure 5). It was discussed that some species survived and multiplied well during the second half of the dry seasons, while others did not do so well. This leads to the hypothesis that the species in the former category had an early start in the season and thus might show an increase in abundance compared with 1973, while the latter category had suffered losses because of the rains and might show a decrease in abundance. Species that had a rate of increase larger than 2 or smaller than 0.5 were classified to their absence in the second half of the dry season (–),
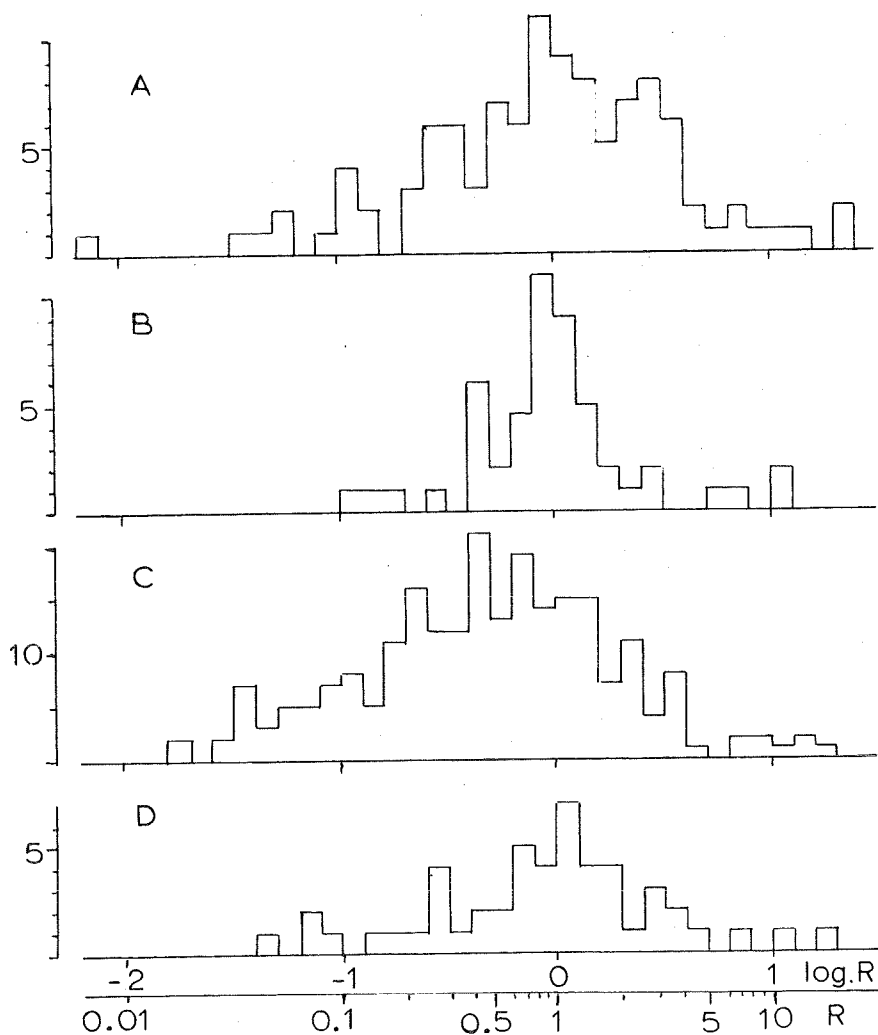
Figure 13 : Distribution of log. R of Homoptera from Panama (A), Homoptera from England and Finland (B), Lepidoptera from England (C) and Carabidae from Netherlands (D). See table 3.

or their presence. The latter category was subdivided according to the degree of presence, just a few individuals (+) or in decent numbers (+). The results are presented in Figure 14. The numbers are low and are not quite satisfactory, but there is a clear tendency for the (-) species to decrease and for the (+) species to increase in abundance in the period from early June to the end of December 1974, as compared with the same period in 1973.

r	PRESENCE WEEK 9-18,1974		
	−	±	+
<0.5	12	4	3
>2.0	3	3	13

Figure 14 : Homoptera that had, between 1973 and 1974, a rate of increase in the traps of more than 2 or smaller than 0.5, classified according to their presence after the rains in the middle of the dry season of 1974, but before the rainy season started. − = absent; + = clearly present; ± = present, but with only a few individuals.

Using the information on all species, mean log. R was calculated for all species in each category. The data are presented in Table 4. The fulgoroids support

TABLE 4

Mean log. R for species that were absent from the traps during the second half of the dry season in 1974 (A), for those there were caught only occasionally during that period in comparison with their abundance during the rest of the year (B), and for those that were caught quite frequently during that period (C). N = number of species in each category; S = variance of the mean; P signifiance level (as determined by the t test) of differences between the means.

					P	
	A	B	C	A–B	B–C	A–C
FLUGOROIDEA						
Mean log. R	−0.343	−0.148	0.276	N.S.	0.01	0.001
S	0.0127	0.0156	0.0063			
N	24	18	32			
CICADELLIDAE and CERCOPOIDEA						
Mean log. R	−0.054	−0.508	0.036	0.05	0.025	N.S.
S	0.0168	0.0208	0.0275			
N	9	6	13			

the hypothesis rather nicely. The species that apparently were able to survive and multiply well during the second half of the dry season had a significantly higher mean rate of increase than those which were present only in very small numbers or did not appear in the traps at all. For the combined data of the cicadellids and cercopids, the story seems to be different. Again, the species that did well during the dry weather show a significantly larger mean rate of increase than those that were present only with a few individuals, but this is due to a pronounced decrease of the latter species, not accompanied by a clear increase of the former. However, this is mostly due to the behavior of the four species of Idiocerinae that all decreased markedly in abundance (mean log. $R = -0.490$) in spite of their presence in the dry season after the rain. Mean log. R of the remaining nine species in this category is 0.2705. These species do show an increase. Mean log. R was not especially low in the species that were absent from the traps in March–April. This major difference between cicadellids and fulgoroids may be due to differences in the way they pass the dry season. As I have discussed before, many fulgoroids may aestivate as nymphs under bark, in the soil, or in logs. Cicadellids, however, may be passing the dry season as nonreproductive adults that are largely nonactive, or as eggs. Some species may just not respond to rain in the dry season and thus are not affected by it (category A), others may become active but die off soon during the dry weather conditions in the following weeks (category B), while still others become active and do well (category C, except the idiocerines). The hypothesis that variations in rainfall pattern do have pronounced effects on many species of homopterans finds rather strong support in the present data. I would, however, feel more confident about this if data become available of a "normal" year; that is, one without strong rains in the dry season (cf. Figure 2).

DISCUSSION

The homopterans in the forest on Barro Colorado Island, Panama Canal Zone, show considerable fluctuation in abundance within a year, and so do any other tropical insects on which I have found data, even if the dry season is much milder than that in Panama (JANZEN, 1973; GIBBS and LESTON, 1970; CLARKE, 1968), or even if there is very little difference in rainfall between the seasons such as in the forest in Sarawak (FOGDEN, 1972). On Barro Colorado Island, my species of homopterans, generally speaking, started to decrease in September/October (well before the end of the rainy season), were low during the dry season, and then had one or more peaks between May and September. There are considerable changes within a season, not just for homopterans, but for most other groups of insects (SMYTHE, in preparation). Comparing the seasons by comparing just one sample from each, as the result will depend on just when those samples were taken. For some spiders in New Guinea (ROBINSON et al., 1974) and some groups of insects in Sarawak (FOGDEN, 1972, Figure 3), areas with a mild, and very mild, dry season respectively, the inimical nature of the dry season is shown by a gradual decrease in abundance. If one had only data from the middle of dry season on Lepidoptera and Hymenoptera in Sarawak and compared these with a rainy season

month such as November, one might very well conclude that the dry season abundance was higher, which would be misleading. It might just be that Janzen's conclusion (1973), about areas with a mild dry season having a peak in abundance of insects in the dry season is erroneous for this reason. What little information there is on insects or spiders in the tropics rather support the hypothesis that where there is a mild dry season, numbers tend to decrease gradually in the dry and increase in the wet season. Where there is a severe dry season, the numbers start declining well before the end of the rainy season, are low in the dry season, and increase in the beginning of the rainy season. As JANZEN (1973) pointed out, there are exceptions to this rule and he gives some examples. Other examples of species that have a peak in abundance in the dry season are given by GIBBS and LESTON (1970). Several tabanids in Zambia (CLARKE, 1968) occur exclusively or have a peak in the last hot months of the dry season. Maybe for such species the dry season is really favorable for adults, maybe it is not. It could be that some species have to produce active adults in a less than favorable season in order to ensure favorable conditions for the larvae, or nymphs, later. Whether or not this is true for the dry season cicadas on BCI is not known.

If the dry season is inimical to adults of most species (either for survival as adults or for reproduction or both) and that is what the evidence suggests, they have evolved some way of coping with the adverse conditions. Whether this adaptation consists of adults going into reproductive diapause, nymphs going into aestivation, or adults moving to more favorable areas, one might expect it to start before the adverse conditions have arrived. Such anticipation of the dry season indeed seems to occur. Some grassland species disperse and are found in the forest traps well before the conditions are really dry (Figure 9) and the same phenomenon occurs with forest species (Figure 10). The general decrease in abundance of homopterans in the last months of the rainy season could suggest that the nymphs already have entered diapause in that period. My data on two species of cercopoids in Las Cumbres, species that have subterranean larvae, suggest that they aestivate as small nymphs and that the first and largest peak in abundance in late May and June cannot have come from eggs produced by the last generation in the previous rainy season. Some proportion of the nymphes produced by earlier generations probably started diapause earlier in the rainy season. JANZEN (1973, p. 695) points out that maintaining an inactive state in a hot site may be rather costly metabolically. The problem, however, is whether it is possible to do it and, if so, whether there are more favorable alternatives. Insects can aestivate. For instance, some weevils in Georgia, USA (TAYLOR et al., 1975) do it during summers that do have an average temperature not much lower and daily maximum temperatures higher than those in Panama. For my homopterans I do not have any direct evidence, but my data suggest that they do aestivate.

The length of the active season (Figure 12) varies enormously. Usually the rainy season is some 32 to 35 weeks long. Of the species included in Figure 12 (BCI), more than 50 percent were present longer than 35 weeks. In fact, the mean of the distribution is at 34.2 weeks. This can be partly attributed to the heavy

rains in the first week of March in 1974. In a normal year, the distribution would be some more to the left. Apparently many species are active for as long as a period as they can. This becomes even more obvious if one takes into account that my estimates of the length of the active dry season may, for several species, be underestimates. Nevertheless, there are species that are active for short periods only. Whether this has to do with their special feeding habits or reproductive strategies is as yet unknown. Such variation also is true for other tropical insects, such as mosquitoes in Panama (GALINDO *et al.*, 1950), tabanids in Zambia (CLARKE, 1968) and heteropterans in Ghana (GIBBS and LESTON, 1970).

In the temperate zone it is freezing weather in the winter that prevents most insects from being active. This is not true for all of them. Some are active during the winter or even have their activity restricted to the winter (DEN BOER, 1967). The summer species are not all active as adults all through the summer months. Of homopterans in England (Figure 12) and Finland (KONTKANEN, 1950), some are, but many others have a much shorter season. The same is true for other insects such as tipulid flies (FREEMAN and ADAMS, 1972). There is quite a bit of overlap in the length of the active season of tropical vs. temperate insects, but, on the average, the seasons in the tropics are much longer. However, if one includes insects from other areas in the comparison–areas that are well outside the tropics but do not have a cold winter, such as homopterans from North Carolina (Figure 12; DAVIS and GRAY, 1966) or aphids from Australia (HUGHES *et al.*, 1965) –the conclusion is that it is not the tropics that are different from nontropical areas, but areas with freezing weather during the winter that are different from the rest. And insects in cold areas that are sheltered from the cold, such as soil arthropods in Scotland (SHEALS, 1957) or England (McFADYEN, 1952) are more comparable in the lengths of their seasons to tropical than to other cold–temperate insects. A reduced level of physical stress during winter or dry season produces, on the average, a longer sustained coexistence of the species (ROBINSON *et al.*, 1974). CLARKE (1968) demonstrates this for the tropics by comparing the seasons of species of tabanids in regions of Africa that differ in length and severity of the dry season. As discussed by ROBINSON *et al.* (1974), the same factors that produced the more sustained coexistence have been cited to have caused a larger species diversity. These authors therefore predict that, other things being equal, there should be a good correlation between the extent of sustained coexistence and species diversity. if any of the hypotheses proposed to explain differences in species diversity on the basis of climatic stability are correct. In most comparisons that can be made with the data discussed here, other things are far from equal. Nevertheless, some comparisons could be relevant to some extent. Homopterans in North Carolina salt marshes (DAVIS and GRAY, 1966) have a much more sustained coexistence than homopterans in grasslands in England (WALOFF, 1971) and Finland (KONT-KANEN, 1950). However, they are not richer in species. The richest fauna of Tabanidae in Africa was found in an area of southern Zambia that had a severe and long dry season with only moderately long active seasons, on the average (CLARKE, 1968). The homopteran fauna on BCI is very rich in species. In Figure 6 are included 160 species of fulgoroids and 82 species of cicadellids. However, several groups

of species, some large, have been left out because of taxonomical difficulties. The actual number of species caught is much larger than these figures suggest. The length of the active season, the degree of sustained coexistence, is not particularly high compared with North Carolina salt marshes where there are only a few species of homopterans. Most of these comparisons leave quite a bit to be desired, some being better than others. However, species with long active seasons are far from restricted to the tropics while areas with a very high species diversity of insects seem to be found only at low latitudes. I do not think that the study lists from a large number of habitats will show any correlation between the lengths of the active seasons and the number of species present. If this is correct, it might be argued that the hypothesis that more equitable benign climates are partly responsible for the large species diversity in the tropics could be wrong and focus more on alternative hypotheses that hold structural complexity of the habitat as partly responsible for the number of species present. For herbivores, such as the homopterans, a factor of importance undoubtedly is the richness of the flora. On Barro Colorado Island, only three miles across, there are some 1400 species of plants (CROAT, in preparation). Why the flora should be this rich I have no idea. JANZEN (1970) proposes an interesting hypothesis, but I am not yet convinced that that is the explanation. Another theoretical possibility would be that in a species–rich ecosystem the species would space out in time in order to reduce interactions between them. RICKLEFS (1966) found that this is not what happens with breeding seasons of birds. Neither is it true for Panamanian homopterans. Most of the species that do have a shorter active season are present in July–September when many species have their peak in abundance.

Some insects in the tropics are present all year round. However, I have found very little evidence for the existence of species that do not fluctuate seasonally. The existing evidence suggest that such species are extremely rare. The only insect species that seem to be almost nonseasonal are some butterflies, such as *Charaxes* spp. in Sierra Leone (OWEN and CHANTER, 1972) and *Heliconius ethilla* in Trinidad (EHRLICH and GILBERT, 1973). Most butterflies do seem to fluctuate in the tropics (EMMEL and LECK, 1970). Among spiders, aseasonal species seem to be more common (ROBINSON *et al.*, 1974; GIBBS and LESTON, 1970). This is not a general contrast between predators and herbivores because, on Barro Colorado Island, mantids and reduviids do fluctuate and so do they in Ghana (GIBBS and LESTON, 1970).

DOBZHANSKY and PAVAN (1950) presented evidence that species of Drosophila in Brazil may show rather large annual changes in abundance The evidence presented in the present paper showns that annual variability of insects in a tropical forest, defined as the variance of the rates of increase of the component species, is remarkably similar to that found elsewhere (Tables 2 and 3, Figure 13). The idea that the tropics might be more constant may have come about by the fact that the temperate species have been chosen for detailed study form a very biased sample of the fauna. Many of them were pest species for forestry or agriculture and thus were chosen because they had very large fluctuations in abundance.

As will be shown in another publication (Wolda and Foster, 1976), such species are by no means absent in a tropical forest.

Tropical forest ecosystems are very rich in species, but do not have a small annual variability and are not especially stable. MAY (1973) showed that there are no mathematical arguments to support the diversity–stability hypothesis. The present paper shows that there is not much factual evidence either.

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